Journal of the Fisheries Research Board of Canada

Journal de l'office des recherches sur les pêcheries du Canada

Volume 32, No. 8, August 1975

Volume 32, n° 8, août 1975

Environment Canada
Fisheries and Marine Service

Environnement Canada
Service des pêches et des sciences de la mer

Journal
of the Fisheries
Research
Board
of Canada

Journal
de l'office
des recherches
sur les pêcheries
du Canada

Environment Canada
Fisheries
and Marine Service
Office of the Editor

Environnement Canada
Service des pêches
et des sciences de la mer
Bureau du Rédacteur

116 Lisgar, Ottawa K1A 0H3

Volume 32, No. 8, August 1975

Volume 32, n° 8, août 1975

The *Journal of the Fisheries Research Board of Canada* has been published continuously since 1901, previously as *Contributions to Canadian Biology* 1901–25, *Contributions to Canadian Biology and Fisheries* 1926–34, and *Journal of the Biological Board of Canada*, 1934–37.

Editorial policy — The *Journal* publishes original research articles and notes, critical reviews, essays of opinion or hypothesis, letters, and book reviews in the broad field of fisheries management, ocean science, and aquatic environments relevant to Canada. Submissions in English or French are accepted without limitations as to origin, but must not have been published or copyrighted and must not be published elsewhere except in abstract form or by written consent of the Editor. The *Journal* accepts no responsibility for statements made by contributors. Details on submissions are given in guides for authors and typists at the back of this issue. Reprints of these guides are available free from the Office of the Editor.

A charge of $30.00 per page is made for manuscripts published. When submitting a manuscript, an author must state that the charge will be accepted.

Subscriptions — The *Journal* is issued monthly to form annual volumes of twelve numbers. Subscription rates are: Canada, $18.00 per year; other countries, $22.00. Single issues are $2.00 and $2.50, respectively. Orders must be sent directly to Information Canada, Ottawa, Canada K1A 0S9, and payment made in Canadian funds to "The Receiver General for Canada."

Microfilm — Issues from 1934 through the current volume can be purchased on 16 or 35 mm microfilm. Photocopies of individual articles or issues can be purchased. Address orders to Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, USA.

Publié depuis 1901, le *Journal de l'office des recherches sur les pêcheries du Canada* a paru sous plusieurs titres: *Contributions to Canada Biology*, 1901–25, *Contributions to Canadian Biology and Fisheries*, 1926–34, et *Journal of the Biological Board of Canada*, 1934–37.

Politique de publication — Le *Journal* publie des articles de recherches, ainsi que des notes, critiques, exposés d'opinions ou d'hypothèses, lettres et recensions concernant le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada. Toutes contributions en français ou en anglais sont acceptées sans restriction quant à la provenance, mais elles ne doivent pas avoir été produites ni avoir fait l'objet d'un copyright et ne doivent pas être publiées nulle part ailleurs sauf sous forme abrégée ou avec le consentement écrit du directeur. Le *Journal* décline toute responsabilité pour ce qui est des affirmations des collaborateurs. Les modalités de présentation des textes font l'objet du guide des auteurs et du guide des dactylos paraissant à la fin du présent numéro. On peut se procurer gratuitement, du bureau du directeur, des exemplaires de ces guides.

Les frais de publication sont de $30.00 la page. Quant un auteur présente un texte, il doit préciser que ces frais seront acceptés.

Abonnement — Le Journal parait tous les mois, formant ainsi un volume de 12 numéros par année. Les frais d'abonnement annuel sont de $18 pour le Canada et de $22 pour les autres pays. Chaque numéro coûte $2.00 au Canada et $2.50 à l'étranger. Prière d'adresser directement les commandes à Information Canada, Ottawa (Ontario), Canada K1A 0S9; les paiements doivent être faits en devises canadiennes, à l'ordre du Receveur général du Canada.

Microfilms — On peut acheter sur microfilms 16 ou 35 mm tous les numéros publiés depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente. Prière d'adresser les commandes à Xerox University Microfilms, 300 North Zeeb Road, Ann Arbor, Michigan 48106, E.-U.

Editor and/Rédacteur et *Director of Scientific Information* *Directeur de l'information scientifique*	J. C. STEVENSON, PH.D.
Deputy Editor *Sous-rédacteur*	J. WATSON, PH.D.
Assistant Editors *Rédacteurs adjoints*	JOHANNA M. REINHART, M.SC. D. G. COOK, PH.D.
Production-Documentation	J. CAMP G. J. NEVILLE/PAULA IRVING
French Abstracts/Résumés français	Y. JEAN, PH.D.

Journal of the Fisheries Research Board of Canada

Volume 32, No. 8, August 1975

Journal de l'office des recherches sur les pêcheries du Canada

Volume 32, n° 8, août 1975

Bacterial Diseases of Fishes: Diagnostic Procedures for Gram-Negative Pathogens

EMMETT B. SHOTTS JR.

Department of Medical Microbiology, College of Veterinary Medicine, University of Georgia, Athens, Ga. 30602, USA

AND G. L. BULLOCK

U.S. Fish and Wildlife Service, Eastern Fish Disease Laboratory, Kearneysville, W. Va. 25430, USA

SHOTTS, E. B. JR., AND G. L. BULLOCK. 1975. Bacterial diseases of fishes: diagnostic procedures for gram-negative pathogens. J. Fish. Res. Board Can. 32: 1243–1247.

A diagnostic scheme employing 10 media, 4 reagents, and 5 specific antiserums has been devised for identification of gram-negative pathogens of fishes. The scheme is not intended for detailed speciation of organisms, but for generic identification of organisms associated with infected fishes. Diagnosis can be accomplished in 24 h with selective media and antiserums, and in no more than 72 h with other media and reagents.

SHOTTS, E. B. JR., AND G. L. BULLOCK. 1975. Bacterial diseases of fishes: diagnostic procedures for gram-negative pathogens. J. Fish. Res. Board Can. 32: 1243–1247.

Un schéma de diagnostique utilisant 10 milieux de culture, 4 réactifs et 5 antisérums spécifiques a été mis au point pour l'identification de bactéries pathogènes Gram-positif des poissons. Le schéma ne vise pas à une identification détaillée à l'espèce, mais plutôt à une identification générique des organismes associés aux poissons infectés. Le diagnostique peut se faire en 24 h avec des milieux sélectifs et des antisérums, et en 72 h ou moins avec d'autres milieux et réactifs.

Received February 24, 1975
Accepted April 22, 1975

Reçu le 24 février 1975
Accepté le 22 avril 1975

INCREASED interest in fish has prompted an awareness of problems associated with their health. The bacterial diseases, particularly those caused by gram-negative organisms, are a major cause of mortality. To aid in the rapid diagnosis of these diseases, investigators have developed a number of schematic keys (Bullock 1971; Glorioso et al. 1974; Lewis 1973). Some of these keys do not take into account the occurrence of certain enteric organisms producing disease in fishes. At present, at least two members of the Enterobacteriaceae have been reported as fish pathogens (Meyer and Bullock 1973; Ross et al. 1966; Wakabayashi and Egusa 1973). As awareness of enteric bacteria in the aquatic environment increases and laboratory

Printed in Canada (J3738)
Imprimé au Canada (J3738)

technology improves, this group of organisms will assume a greater role in fish disease diagnostics. Therefore, procedures for detecting all gram-negative bacterial fish pathogens should be expanded.

In diagnostic work, the ideal is to obtain an accurate diagnosis with a minimum expenditure of time, effort, and equipment. In our procedures, 17 genera of gram-negative bacteria can be identified by using 10 media, 4 reagents, and 5 specific hyperimmune serums. With some exceptions, we chose to keep our identification procedures at the generic rather than at the specific levels. In most disease situations in fish, either a single species is responsible for the disease, or the complex of species responsible is not clearly understood.

Materials and Methods

SELECTION OF SPECIMENS

Several typical moribund specimens should be examined, but dead fish should never be used for diagnostic purposes due to rapid postmortem proliferation of endogenous bacteria into the tissues (Bullock 1971; Heuschmann-Brunner 1970). As has been described (Bullock 1971), the first step in diagnostic examination is to determine if bacteria are present in affected tissues. Gram-stained smears are examined from kidney or other internal organs, if a septicemia is suspected, or from gill or fin tissue if the disease is external. It should be stressed that fins, gills, or external lesions always contain several types of bacteria in addition to the suspected pathogen.

The gram-stained smear establishes whether the disease is caused by a gram-negative bacterium and also the type of pathogen involved — short rods characteristic of Aeromonads, Pseudomonads, and enterics, or long thin rods characteristic of myxobacteria. From this information a decision can be made as to which of the four primary plating media should be used (Fig. 1). Myxobacteria can be distinguished morphologically from the short gram-negative rods and cultured on *Cytophaga* agar (Bullock 1971). Short gram-negative rods can be cultured on any of three media: Pseudosel (BBL — Baltimore Biological Laboratories, BioQuest Corporation, P.O. Box 243, Cockeysville, Md. 21030) and Rimler-Shotts media (Shotts and Rimler 1973) are both selective, whereas all of the most frequently encountered gram-negative bacteria can be cultured on Tryptic Soy Agar (Difco Laboratories, Inc., Detroit, Mich. 48232) or Trypticase Soy Agar (TSA) (BBL).

MEDIA AND REAGENTS

We suggest the following media for the major gram-negative bacterial pathogens:

A. Primary isolation, dependent upon cellular morphology:
   1. Pseudosel (BBL)
   2. Trypticase Soy Agar (BBL) or Tryptic Soy Agar (Difco)
   3. Rimler-Shotts (RS) Agar
   4. *Cytophaga* Agar

B. Specific media for aiding presumptive identification of isolates:
   1. Oxidation/fermentation (O/F) basal medium (Difco) with 1% glucose added
   2. Moeller decarboxylase broth base (BBL or Difco) with 1% l-lysine added
   3. Triple sugar iron (TSI) agar (BBL or Difco)
   4. Tryptone broth, BBL, or Dfco (for motility and indol production)
   5. MR-VP broth, BBL, or Difco (for acetyl–methyl carbinol production)
   6. Urea agar, BBL, or Difco (for urease production)

C. Reagents and supplies used for identification:
   1. Cytochrome oxidase strips (Warner-Chilcott, Inc.)
   2. Novobiocin sensitivity discs, 10 μg level (BBL, Difco)
   3. Kovac's reagent for indol
   4. Voges-Proskauer reagents for acetyl–methyl carbinol detection
   5. Specific hyperimmune antiserums for:
      a. Enteric (Hagerman) redmouth bacterium
      b. *Chondrococcus columnaris*
      c. *Cytophaga psychrophila*
      d. *Aeromonas salmonicida*
      e. *Vibrio anguillarum*

These antiserums should be prepared by the investigator. Limited quantities for reference purposes may be obtained from the Eastern Fish Disease Laboratory, Kearneysville, W.Va., 25420 USA.

Identification of the Short Gram-Negative Rods

If short gram-negative rods are found, one or more primary plating media can be streaked. Whether or not all three media are used will depend on the experience of the investigator.

Pseudosel agar is recommended as a primary medium for the isolation of pseudomonads because the presence of cetrimide in this medium effectively inhibits most other gram-negative organisms. An incubation temperature of 20 C is favorable for isolation of *Pseudomonas fluorescens*, which appears to be the most prevalent type of pseudomonad in diseased fish (Bullock et al. 1965). Pseudomonads can be further confirmed by using cytochrome oxidase and O/F glucose (Bullock 1964).

To ensure isolation of all major psychrophilic or mesophilic organisms, one can inoculate Trypticase Soy Agar or Tryptic Soy Agar and incubate the cultures at both 20 and 35 C. Each colony type obtained must be examined for motility, cytochrome oxidase, and the presence of distinct diffusible brown pigmentation at 20 C. If crowding or overgrowth occurs, restreaking is necessary to

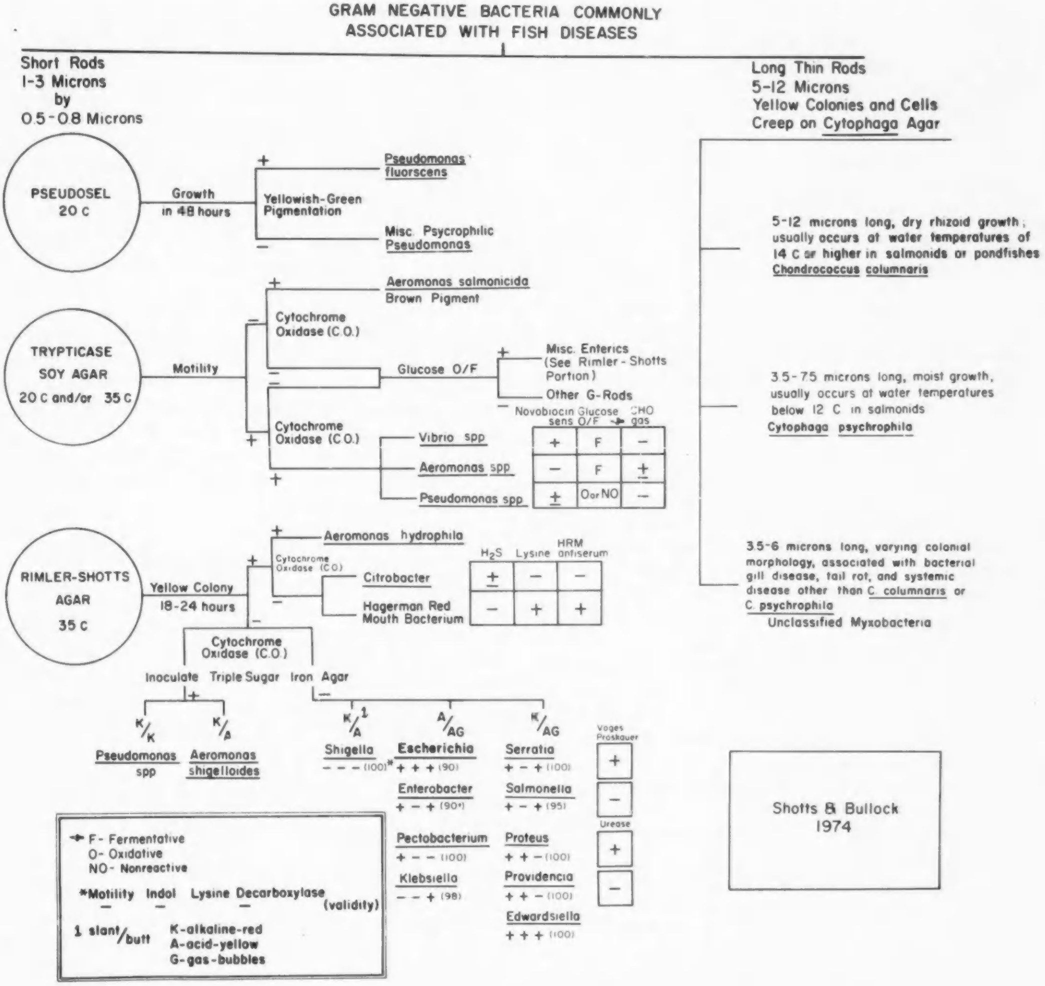

GRAM NEGATIVE BACTERIA COMMONLY ASSOCIATED WITH FISH DISEASES
Short Rods 1-3 Microns by 0.5-0.8 Microns
Long Thin Rods 5-12 Microns Yellow Colonies and Cells Creep on Cytophaga Agar
PSEUDOSEL 20 C
Growth in 48 hours
Yellowish-Green Pigmentation
+
Pseudomonas fluorscens
−
Misc. Psycrophilic Pseudomonas
TRYPTICASE SOY AGAR 20 C and/or 35 C
Motility
Cytochrome Oxidase (C.O.)
Aeromonas salmonicida Brown Pigment
Glucose O/F
Misc. Enterics (See Rimler-Shotts Portion)
Other G-Rods
Novobiocin sens
Glucose O/F
CHO gas
Vibrio spp
+ F −
Aeromonas spp
− F ±
Pseudomonas spp
± O or NO −
RIMLER-SHOTTS AGAR 35 C
Yellow Colony 18-24 hours
Aeromonas hydrophila
H2S Lysine HRM antiserum
Citrobacter
± − −
Hagerman Red Mouth Bacterium
− + +
Inoculate Triple Sugar Iron Agar
K/K Pseudomonas spp
K/A Aeromonas shigelloides
K/A 1 Shigella − − − (100)*
A/AG Escherichia + + + (90)
Enterobacter + − + (90+)
Pectobacterium + − − (100)
Klebsiella − − + (98)
K/AG Serratia + − + (100)
Salmonella + − + (95)
Proteus + + − (100)
Providencia + + − (100)
Edwardsiella + + + (100)
Voges Proskauer + −
Urease + −
F- Fermentative
O- Oxidative
NO- Nonreactive
*Motility Indol Lysine Decarboxylase (validity)
1 slant/butt K-alkaline-red A-acid-yellow G-gas-bubbles
5-12 microns long, dry rhizoid growth; usually occurs at water temperatures of 14 C or higher in salmonids or pondfishes Chondrococcus columnaris
3.5-7.5 microns long, moist growth, usually occurs at water temperatures below 12 C in salmonids Cytophaga psychrophila
3.5-6 microns long, varying colonial morphology, associated with bacterial gill disease, tail rot, and systemic disease other than C. columnaris or C. psychrophila
Unclassified Myxobacteria
Shotts & Bullock 1974

FIG. 1. Differentiation of the major gram-negative pathogens of fishes by use of morphology, differential media, and selected biochemic and serologic tests.

ensure proper evaluation. Colonies demonstrating brown pigmentation and cytochrome oxidase activity, but no motility, are usually *Aeromonas salmonicida.* Definitive identification may be accomplished by agglutination with specific antiserum.

Cytochrome oxidase positive colonies of motile organisms should belong to one of the following:

A. Nonhalophilic *Vibrio* spp., principally *V. anguillarum*
B. *Aeromonas hydrophila* complex
C. *Pseudomonas* spp.

These groups may be further delineated by novobiocin sensitivity and by their reaction in glucose O/F medium. Some taxonomists consider the *Aeromonas hydrophila* complex to be composed of aerogenic and anaerogenic forms (Ewing et al. 1961). In our experience the aerogenic form is the more commonly encountered in diseased fish; however, on rare occasions the anaerogenic form is isolated. Anaerogenic aeromonads should be differentiated from anaerogenic *Vibrio* spp. (Bullock 1964).

Other cytochrome oxidase positive organisms demonstrating pigmentation — yellow, nondiffusible (*Flavobacterium* sp. or *Xanthomonas* spp.) or purple (*Chromobacterium* sp.) — are not considered here since their present role in fish disease is minor (Lewis 1973).

All oxidase negative isolates, regardless of pigmentation or motility, should be inoculated into glucose O/F medium.

Isolates that ferment glucose should be presumptively considered as belonging to the family Enterobacteriaceae. Nonfermenters or oxidative organisms will not be considered further here because their role in fish diseases is minor.

The recent development of Rimler-Shotts (RS) medium for isolation of the *Aeromonas hydrophila* complex has facilitated identification of this group (Rimler et al. 1974), and presumptive selection of various members of the family Enterobacteriaceae.

Recovery after 18–24 h of yellow colonies that are not interspersed with black-centered yellow colonies is highly suggestive of the presence of the *Aeromonas hydrophila* complex, especially if the yellow colonies are cytochrome oxidase positive. Since cytochrome oxidase reaction is inhibited by the presence of acid, suspect colonies should be grown on TSA before they are tested.

Yellow colonies that are cytochrome oxidase negative should be considered as either possible *Citrobacter* spp. or as the as yet-unclassified enteric organism causing Enteric (Hagerman) redmouth disease (ERM).

Citrobacter spp. and the ERM organism may be separated further by:

A. Hydrogen sulfide (H_2S) production
B. Lysine decarboxylation
C. Agglutination in specific antiserum

All nonyellow cytochrome oxidase negative colonies (bluish-green with or without H_2S) should be considered presumptively as members of the family Enterobacteriaceae. Representative colony types should be inoculated into triple sugar iron agar. Characteristic TSI reactions afford tentative grouping of recovered enterics. They may be further delineated into genera by determination of:

A. Motility
B. Indol production
C. Lysine decarboxylation
D. Urease production
E. Acetyl–methyl carbinol production

On rare occasions, nonyellow cytochrome oxidase positive colonies may be encountered. Such colonies usually represent either mesophilic pseudomonads or anaerogenic aeromonads (*A. shigelloides*), which may be separated by TSI reaction.

Identification of the Long Gram-Negative Rods

The presence of long thin gram-negative rods in infected fish tissue indicates a probable myxobacterial infection. As indicated in Fig. 1, specific myxobacteria have been demonstrated for only two diseases. *Chrondrococcus columnaris* and *Cytophaga psychophila* may be presumptively identified on the basis of cell length, colony appearance on *Cytophaga* agar, and the temperature range at which the disease occurs. Agglutination tests with specific antiserum insures definitive identification.

Fish diseases such as bacterial gill disease and fin rot are associated with myxobacteria. Large numbers of the latter are seen in stained smears of infected gill or fin tissues but they have not been shown to be specific etiologic agents. Whether or not myxobacteria are primary or secondary agents, they are associated with significant mortality among both warmwater and coldwater fishes.

Discussion

The described procedures have been used with success in both our laboratories and we believe that, although the scheme will not group all gram-negative pathogens encountered in fish, it will accurately identify most isolates. In our estimation, no dubious criteria are included in this scheme. Caution, however, should be exercised in following closely the recommended incubation time and temperature. Similarly, care should be taken to ensure the maintenance of a high moisture content in the *Cytophaga* agar, because dehydration will retard the development and spread of colonies.

The use of several antiserums has been suggested as a final confirmatory step in identification.

It should be emphasized that this scheme is not intended for detailed speciation of organisms. Rather, it is designed to provide rapid identification of organisms associated with disease processes with little delay and with high assurance that the information obtained can be rapidly integrated into the correction of the disease problem.

The proposed scheme requires relatively few media, reagents, and specific antiserums. Usually diagnosis can be accomplished in as few as 24 h with the selective media and in no more than 72 h with other media and reagents.

BULLOCK, G. L. 1964. *Pseudomonadales* as fish pathogens. Dev. Ind. Microbiol. 5: 101–108.

1971. Identification of fish pathogenic bacteria, p. 1–196. *In* S. F. Snieszko and H. R. Axelrod [ed.] Diseases of fish — bacteria. T. F. H. Publications, Inc., Neptune City, N.J.

BULLOCK, G. L., S. F. SNIESZKO, AND C. E. DUNBAR. 1965. Characteristics and identification of oxidative pseudomonads isolated from diseased fish. J. Gen. Microbiol. 38: 1–7.

EWING, W. H., R. HUGH, AND J. G. JOHNSON. 1961. Studies on the Aeromonas group. U.S. Dep. Health Educ. Welfare, Public Health Serv. Communicable Dis. Cent. Monogr. 37 p.

GLORIOSO, J. C., R. L. AMBROSKI, J. M. LARKIN, G. F. AMROSKI, AND D. C. CULLEY. 1974. Laboratory identification of bacterial pathogens of aquatic animals. Am. J. Vet. Res. 35: 447–450.

HEUSCHMANN-BRUNNER, G. 1970. Untersuchungen uber die Vermehrung der Aeromonaden im toten Fischkorper. Tieraerztl. Wochenschr. 83(19): 381–384.

LEWIS, D. H. 1973. Predominant aerobic bacteria of fish and shellfish. Texas A & M Univ., College Station, Texas. 102 p.

MEYER, F. P., AND G. L. BULLOCK. 1973. *Edwardsiella tarda*, a new pathogen of channel catfish (*Ictalurus punctatus*). Appl. Microbiol. 25: 155–156.

RIMLER, R. B., E. B. SHOTTS, AND P. GHITTINO. 1974. Infections *Aeromonas hydrophila* chez les poissons: diagnostic rapide a l'aide du milieu. R. S. Cah. Med. Vet. 43: 47–52.

ROSS, A. J., R. R. RUCKER, AND W. H. EWING. 1966. Description of a bacterium associated with redmouth disease of rainbow trout (*Salmo gairdneri*). Can. J. Microbiol. 12: 763–770.

SHOTTS, E. B., AND R. B. RIMLER. 1973. Medium for the isolation of *Aeromonas hydrophila*. Appl. Microbiol. 26: 550–553.

WAKABAYASHI, H., AND S. EGUSA. 1973. *Edwardsiella tarda* (*Paracolobactrum anguillimortiferum*) associated with pond-cultured eel disease. Bull. Jap. Soc. Sci. Fish. 39: 931–936.

Isolation and Identification of Constituents Toxic to Juvenile Rainbow Trout (*Salmo gairdneri*) in Caustic Extraction Effluents from Kraft Pulpmill Bleach Plants

J. M. LEACH AND A. N. THAKORE

B.C. Research, Vancouver, B.C. V6S 2L2

LEACH, J. M., AND A. N. THAKORE. 1975. Isolation and identification of constituents toxic to juvenile rainbow trout (*Salmo gairdneri*) in caustic extraction effluents from kraft pulpmill bleach plants. J. Fish. Res. Board Can. 32: 1249–1257.

Chemical constituents in effluent from the caustic extraction stage of the bleach plant at a western Canada kraft pulpmill were fractionated to identify factors responsible for their toxicity to juvenile rainbow trout (*Salmo gairdneri*). At all stages in the fractionation procedure bioassays were carried out to monitor toxicities of the isolated materials. Five toxic compounds, separated in a pure state from the effluent, were characterized by chromatography, spectroscopy, and chemical synthesis. The compounds and their 96-h median lethal concentrations (LC50) measured in static bioassays were: 3,4,5-trichloroguaiacol (0.75 mg/liter), 3,4,5,6-tetrachloroguaiacol (0.32 mg/liter), monochlorodehydroabietic acid (0.6 mg/liter), dichlorodehydroabietic acid (0.6 mg/liter), 9,10-epoxystearic acid (1.5 mg/liter).

The same compounds were shown to be present in caustic extraction effluents collected from six other western kraft mills. For two samples, the concentration–toxicity graphs from bioassays of solutions containing only the pure toxicants in the amounts found by analysis were similar to those of the actual effluents produced by the mills. Concentrations of the toxic constituents in samples from six different mills were equivalent to 2.3–24 TU (toxic units), confirming that they are important factors in the toxicity of caustic extraction effluents.

LEACH, J. M., AND A. N. THAKORE. 1975. Isolation and identification of constituents toxic to juvenile rainbow trout (*Salmo gairdneri*) in caustic extraction effluents from kraft pulpmill bleach plants. J. Fish. Res. Board Can. 32: 1249–1257.

Nous avons fractionné les constituants chimiques de l'effluent produit à la phase d'extraction caustique dans l'installation de blanchiment d'une usine de pâte à papier kraft de l'ouest canadien, dans le but d'identifier les facteurs responsables de leur toxicité à l'endroit de jeunes truites arc-en-ciel (*Salmo gairdneri*). Des essais biologiques furent effectués à tous les stades du processus de fractionnement en vue d'assurer un contrôle continu de la toxicité des matériaux isolés. On détermina les caractéristiques de cinq composés toxiques isolés de l'effluent à l'état pur, par chromatographie, spectroscopie et synthèse chimique. Ces composés, ainsi que leurs concentrations létales médianes après 96 h (CL50) mesurées lors d'essais biologiques statiques, sont les suivants: 3,4,5-trichloroguaïacol (0.75 mg/litre), 3,4,5,6,-tétrachloroguaïacol (0.32 mg/litre), acide monochlorodéshydroabiétique (0.6 mg/litre), acide dichlorodéshydroabiétique (0.6 mg/litre), acide 9,10-époxystéarique (1.5 mg/litre).

Les mêmes composés sont présents dans les effluents d'extraction caustique de six autres papeteries kraft de l'ouest. Pour deux échantillons, les graphiques concentration–toxicité résultant d'essais biologiques de solutions ne contenant que les toxiques purs en quantités observées par analyse sont semblables à ceux d'effluents réels produits par les papeteries. Les concentrations des constituants toxiques dans les échantillons de six usines différentes équivalent à 2.3–24 unités toxiques, confirmant le fait qu'ils sont des facteurs importants dans la toxicité d'effluents d'extraction caustique.

Received January 8, 1975
Accepted March 20, 1975

Reçu le 8 janvier 1975
Accepté le 20 mars 1975

NEUTRALIZED, raw bleach plant effluents from kraft pulpmills are acutely toxic to fish. The effluents contain dissolved lignin and cellulose degradation products from reactions between bleaching chemicals and the pulp. In a typical process, the unbleached pulp, or brownstock, becomes fully bleached in five (or six) sequential stages, designated CE(H)DED, where C is chlorination, E is caustic extraction, H is hypochlorite, and D is chlorine dioxide. Effluents produced by washing the pulp after each stage are usually combined into acid and caustic streams before being sewered.

Printed in Canada (J3689)
Imprimé au Canada (J3689)

Howard and Walden (1971) found that caustic extraction effluent was the most toxic of the major kraft process streams in a survey of seven British Columbia mills. Betts and Wilson (1966), on the other hand, concluded that chlorination-stage effluent was the most toxic stream at a New Brunswick mill. Little is known of the chemical constituents that are responsible for the toxicity of kraft bleachery wastes. Servizi et al. (1968) suggested that chlorinated catechols could be toxic factors, but there has been no confirmation of their existence in bleaching effluents. Das et al. (1969) provided evidence implicating tetrachloro-*o*-benzoquinone as a toxic constituent of chlorination-stage effluent. Nothing has been published on the nature of the toxic materials in caustic bleachery effluents.

A study was therefore carried out to isolate and characterize the toxic constituents in kraft mill caustic extraction effluent. Chemical fractions separated from the effluent were monitored for toxicity to juvenile rainbow trout (*Salmo gairdneri*) at all stages of a fractionation procedure based on chromatographic techniques. This paper contains details of the toxicants that were identified.

Materials and Methods

APPARATUS

Extracts and pure isolates from caustic extraction effluent were analyzed by gas–liquid chromatography (GC) and thin layer chromatography (TLC) before and after methylation with diazomethane. GC was carried out on Perkin-Elmer Model 881 or 3920 instruments fitted with flame-ionization detectors. Stainless steel (SS) columns (6 ft × ⅛ inch) were used containing the following stationary phases (10% wt/wt) on 100–120 mesh Gas Chrom P: EGSS-X, SILAR-10C, OV-17, SE-30. Temperature programming was usually 150–220 C at 2 C/min, He flowrate 10–20 ml/min. Preparative GC was done on a Varian Associates Autoprep instrument containing a 6 ft × ¼ inch SS column packed with 10% EGSS-X on acid-washed, DMCS-treated Chromosorb W at 220 C, N_2 flowrate 60 ml/min. Analytical TLC was carried out on 0.2-mm silica gel precoated plates (Brinkmann Instruments F-254) and preparative separations were on 0.5-mm layers.

Infrared (IR) spectra were obtained on a Perkin-Elmer Model 521 instrument. Proton nuclear magnetic resonance (NMR) spectra were run on samples dissolved in deuteriochloroform, using a Varian A-60 instrument. Chemical shifts (δ) are quoted relative to tetramethylsilane; signals are recorded as singlets (s), doublets (d), triplets(t), or multiplets (m). Combination GC–mass spectrometry (MS) was carried out using a 10% SILAR-10C column in a Varian Associates Model 1400 Aerograph GC connected via a glass interface to a Hitachi Perkin-Elmer RMU-6E mass spectrometer. Melting points (mp) were measured on a Kofler Hot Stage instrument.

FRACTIONATION PROCEDURE

The fractionation scheme is summarized in Fig. 1.

First-stage caustic extraction effluent (160 liters), pH 10.8, collected from a B.C. Interior kraft mill during a 2-h period of steady operation, was passed at a rate of approximately 30 ml/min for 16 h through six glass columns containing Amberlite XAD-2 resin (22 liters; Rohm and Haas Company). Other conditions were described previously for a similar study on kraft mill unbleached whitewater (Leach and Thakore 1973). Material adsorbed by the resin, and residual effluent trapped in the interstices of the resin, were eluted by 10:1 diethyl ether–methanol. The organic layer was separated from the aqueous layer, solvent was evaporated and the residue obtained was combined with material extracted from the aqueous phase for 24 h by diethyl ether. The extract was dried under reduced pressure over KOH pellets to give a dark brown oil (11.33 g). A portion of the oil (10.55 g) was dissolved in diethyl ether and extracted with 5% aqueous NaOH. The ether layer yielded a nonacidic fraction (2.91 g). The alkaline extract was adjusted first to pH 6, and then to pH 2, and was extracted at both pH's with ether to give an acidic fraction (7.57 g).

The acidic fraction (6.49 g) was divided into four equal portions and each was chromatographed on a column of 60–200 mesh silica gel (100 g; HiFlosil, Applied Science Laboratories) using stepwise elution with $CHCl_3$, mixtures of $CHCl_3$ with 1, 3, and 5%

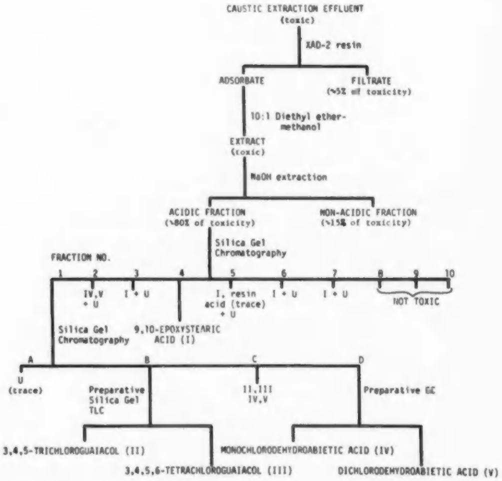

CAUSTIC EXTRACTION EFFLUENT (toxic)
XAD-2 resin
ADSORBATE
FILTRATE (~5% of toxicity)
10:1 Diethyl ether-methanol
EXTRACT (toxic)
NaOH extraction
ACIDIC FRACTION (~80% of toxicity)
NON-ACIDIC FRACTION (~15% of toxicity)
Silica Gel Chromatography
FRACTION NO.
1
2
3
4
5
6
7
8
9
10
IV,V + U
I + U
I, resin acid (trace) + U
I + U
I + U
NOT TOXIC
Silica Gel Chromatography
9,10-EPOXYSTEARIC ACID (I)
A
B
C
D
U (trace)
Preparative Silica Gel TLC
II,III IV,V
Preparative GC
3,4,5-TRICHLOROGUAIACOL (II)
3,4,5,6-TETRACHLOROGUAIACOL (III)
MONOCHLORODEHYDROABIETIC ACID (IV)
DICHLORODEHYDROABIETIC ACID (V)

FIG. 1. Fractionation scheme for caustic extraction effluent. U = unidentified constituent(s).

CH_3OH, then CH_3OH alone, and finally 10% aqueous NaOH. Approximately 50 aliquots (20 ml) were obtained from each chromatography and they were combined on the basis of TLC analysis to give 12 fractions. Two of the fractions were chromatographed again on silica gel developed with C_6H_6, mixtures of C_6H_6 with 5 and 10% CH_3OH, then CH_3OH. Ten fractions, coded Fractions 1–10 (Fig. 1), were eventually obtained.

Fraction 1 (412 mg) was divided into Fractions A–D by silica gel chromatography using stepwise elution with mixtures of petroleum ether (bp 30–60 C), C_6H_6 and CH_3OH. Fraction B (90 mg) was separated into 3,4,5-trichloroguaiacol (47 mg) and 3,4,5,6-tetrachloroguaiacol (25 mg) by preparative silica gel TLC using C_6H_6, CH_3OH, acetic acid (50/8/4) as the solvent. GC retention times, IR, NMR, mass spectra, and melting points were identical with synthesized samples of the guaiacols. Fraction D was methylated with diazomethane and the constituents were separated by preparative GC into methyl monochlorodehydroabietate and methyl dichlorodehydroabietate. GC retention times, IR, NMR, and mass spectra were identical with those of synthetically prepared samples.

Fraction 4 was a single component by GC and TLC and was identified from MS data (Ryhage and Stenhagen 1960) as 9,10-epoxystearic acid. IR and NMR spectra and the mp were in agreement with those of a synthesized sample.

SYNTHESIS OF TOXICANTS

Toxic constituents isolated from caustic extraction effluent were synthesized by the following procedures.

9,10-Epoxystearic acid — Obtained by treatment of oleic acid in $CHCl_3$ with *m*-chloroperbenzoic acid at 20 C for 4 h. The epoxide was crystallized from petroleum ether. Yield 85%. Mp 58–59 C (lit. 58.1–58.7 C; Witnauer and Swern 1950); IR (film) 1690, 1260, 928, 845 cm^{-1}; NMR, δ 9.67 (1H, broad s, D_2O exchangeable), 2.93 (2H,m,cis-epoxide; Aplin and Coles 1967), 2.37 (2H,t,J=6.5Hz), 1.32–1.42 (27H,m), 0.89–0.97 (2H,m); mass spectrum, m/e 298 (M^+), 155 (base peak), 120, 185, 156, 256, 213 The mass spectrum of the methyl ester was identical with published data (Ryhage and Stenhagen 1960).

Monochlorodehydroabietic acid — Synthesized from dehydroabietic acid by addition of chlorine (1 mol equivalent) and a crystal of ferric chloride in CCl_4 at 20 C with exclusion of light. The product was treated with 2-amino-2-methyl-1-propanol and the resulting salt was crystallized from acetone. Monochlorodehydroabietic acid was obtained as a mixture of isomers (yield 36%) on acid-hydrolysis of the amine salt. The isomeric methyl esters gave two peaks on GC (SILAR-10C) and the mixture had the following spectral details: IR ($CHCl_3$) 2930–2970, 1721, 1460, 1250, 1135 cm^{-1}; NMR, δ 7.14 (2H,s, aromatic), 3.70 (3H,s,CO_2CH_3), 1.28 (3H,s,C-4 CH_3), 1.23 (6H,d,J=7Hz,$C(CH_3)_2$), 1.20 (3H,s, C-10 CH_3); mass spectrum m/e 348 (M^+), 273 (base peak), 275, 274, 333, 207, 181. Mass measurement, M^+ 348.184; calculated for $C_{21}H_{29}O_2Cl$, 348.193.

Dichlorodehydroabietic acid — Obtained by adding a molar excess of chlorine to a solution of dehydroabietic acid and $FeCl_3$ in CCl_4 at 20 C in the dark. Yield 33%. Mp 218–220 C. Spectral details for methyl ester: IR ($CHCl_3$) 2940, 1723, 1460, 1250, 1136 cm^{-1}; NMR, δ 7.18 (1H,s,aromatic), 3.68 (3H, s,CO_2CH_3), 1.41 (6H,d,J=7Hz,$C(CH_3)_2$), 1.27 (3H, s,C-4 CH_3), 1.20 (3H,s,C-10 CH_3); mass spectrum, m/e 382 (M^+), 307 (base peak), 309, 241, 308; mass measurement, M^+ 382.144; calculated for $C_{21}H_{28}O_2Cl_2$, 382.146.

3,4,5-Trichloroguaiacol — Prepared from guaiacol using conditions similar to those described by Sarkanen and Dence (1960). Mp 105–107 C (lit. 107–108 C; Heilbron and Bunbury 1953); IR ($CHCl_3$) 3525, 1598, 1480, 1272, 1052 cm^{-1}; NMR, δ 6.90 (1H,s,aromatic), 5.90 (1H,s,D_2O exchangeable), 3.91 (3H,s,OCH_3); mass spectrum, m/e 226 (M^+, base peak), 228 (M + 2), 230 (M + 4), ratio 3:3:1, 211, 183, 147, 113. Methyl ether (3,4,5-trichloroveratrole): mass spectrum, m/e 240 (M^+, base peak), 242 (M + 2), 244 (M + 4), 225, 162, 197, 147.

3,4,5,6-Tetrachloroguaiacol — Synthesized from guaiacol by the method of Sarkanen and Dence (1960). Mp 119–120 C (lit. 119–121 C); IR ($CHCl_3$) 3518, 1570, 1420, 1396, 1020 cm^{-1}; NMR, δ 6.00 (1H,s,D_2O exchangeable), 3.97 (3H,s,OCH_3); mass spectrum, m/e 260 (M^+), 262 (M + 2), 264 (M + 4), 266 (M + 6), ratio 1:1.3:0.6:0.1, 246 (base peak), 244, 219, 183. Methyl ether (3,4,5,6-tetrachloroveratrole): mass spectrum, m/e 274 (M^+, base peak), 276 (M + 2), 278 (M + 4), 206, 261, 218.

BIOASSAYS

Toxicities of effluents, extracts, and pure compounds were measured at 12 ± 1 C in static bioassays using glass aquaria containing 11 juvenile rainbow trout (*Salmo gairdneri*) in 3 or 6 liters of solution. Static bioassays without solution exchange were done because of the limited quantities of isolates and pure toxicants available. Stock fish were maintained at 11 ± 1 C in a population density less than 4 liters/g per day. Mean body weight increased from 0.17 to 0.38 g during the period required to isolate the effluent constituents, but fish loadings in bioassays were always less than 1 g/liter. Dilutions were made with dechlorinated water (pH 6.4, EDTA hardness 6 mg $CaCO_3$/liter) and solutions were maintained at pH 6.4 with McIlvaine's buffer (8 ml/liter; Anon. 1947). DO was kept above 8 mg/liter by gentle aeration.

Extracts and pure compounds were dissolved in CH_3OH (5 ml), 10% NaOH (5 ml) was added and, where necessary, a few drops of Miranol J2M dispersant. Solutions were made to a standard volume with dechlorinated water and aliquots were pipetted for bioassays. Control bioassays containing 30 ml/liter CH_3OH, 50 mg/liter Miranol J2M, and 16 ml/liter buffer were not toxic to the fish.

TABLE 1. Kraft mill bleach plant operating conditions.

Wood species (%)	Spruce 60, pine 16, balsam 12, fir 10, hemlock 2
Bleached pulp production	810 tons/day
Kappa no. of unbleached pulp	19.6–21.2
Bleaching sequence	CEDED
Chlorination stage (C)	
Chlorine applied to pulp	4.7%
Chlorine dioxide applied to pulp	nil
Temperature	82 F
Residual Chlorine	0.05–0.13 g/liter
1st caustic extraction stage (E)	
NaOH applied to pulp	4.7–5.0%
Temperature	190 F
Wash water	50% fresh water, 50% recycled E-stage effluent
Effluent flow	1500 gpm

Results

ISOLATION OF TOXICANTS

Five important toxic constituents of kraft mill caustic extraction effluent were isolated and characterized. The compounds were: 3,4,5-trichloroguaiacol, 3,4,5,6,-tetrachloroguaiacol, monochlorodehydroabietic acid, dichlorodehydroabietic acid, 9,10-epoxystearic acid.

Mill operating data for the day the sample was collected are shown in Table 1. Bleaching conditions were similar to those used in many kraft mills. The fractionation scheme used to isolate the toxicants is outlined in Fig. 1. Bioassays using juvenile rainbow trout were carried out at each stage of the fractionation and the results plotted as logarithmic concentration–toxicity graphs are shown in Fig. 2.

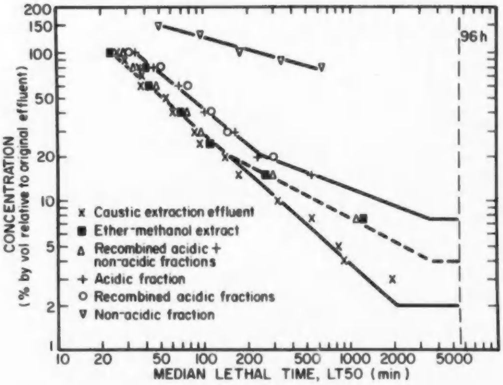


FIG. 2. Concentration–toxicity relationships of caustic extraction effluent and separated fractions.

Materials in the effluent after percolating through XAD-2 resin were only as toxic as a 5% solution of the original effluent. Constituents adsorbed from the effluent by the resin were eluted in ether–methanol and gave a concentration–toxicity graph that deviated from the caustic extraction effluent curve only at low concentrations, as expected from the small toxicity leakage in the initial adsorption stage. Acidic and nonacidic fractions were then separated from the ether–methanol extract. The major portion of the overall caustic extraction effluent toxicity was present in the acidic fraction. When acidic and nonacidic fractions were recombined in the concentrations that they occurred in the original effluent, the toxicity curve was identical with that obtained for the ether–methanol extract. Thus, no toxicity loss occurred at this stage of the separation.

Column chromatography of the acidic fraction on silica gel gave 10 fractions having the TLC patterns shown in Fig. 3. GC–MS analysis of each fraction led to tentative identification of several compounds. Some material losses were incurred during the chromatography, but bioassays of the 10 acidic fractions, after their recombination in the correct concentrations relative to the original effluent, indicated that toxicity losses were minimal (Fig. 2).

Each of the 10 acidic fractions was then tested separately for toxicity at 5 times the concentration that it occurred in the caustic extraction effluent. The results are given in Table 2. Fractions 1 and 4 were the most toxic and were examined in detail.

Fraction 1 was chromatographed on a column of silica gel to give four subfractions, A–D (Fig. 1). Fraction A contained only a trace amount of material and was not examined further. 3,4,5-Trichloro- and 3,4,5,6-tetrachloro-guaiacol were isolated from Fraction B by preparative TLC

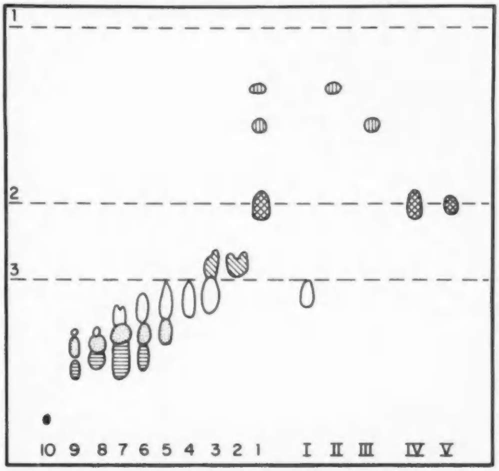


FIG. 3. TLC of acidic fractions. Support: Silica gel. Solvents: 1, 90% $CHCl_3$, 10% petroleum ether; 2, $CHCl_3$; 3, 90% $CHCl_3$, 10% CH_3OH. Acidic fractions 1–10; standards: I,9,10-epoxystearic acid; II,3,4,5-trichloroguaiacol; III,3,4,5,6-tetrachloroguaiacol; IV,-monochlorodehydroabietic acid; V,dichlorodehydroabietic acid.

and were characterized spectroscopically and by synthesis from guaiacol. Fraction D was methylated and then was separated by preparative GC into methyl monochloro- and methyl dichlorodehydroabietate, which were identified by comparison of their IR, NMR, and mass spectra with those of synthesized samples. Fraction C was a mixture of the four chlorinated compounds. The isolated and the synthesized samples of monochlorodehydroabietate gave two peaks on GC (SILAR-10C). NMR analysis indicated that the peaks were due to isomers with chlorine at different positions in the aromatic ring; the mass spectra were identical. Methyl dichlorodehydroabietate was a single compound by GC (SILAR-10C). Neither of the dehydroabietic acid derivatives has been reported in the literature. The positions of chlorine-substitution in the aromatic ring are under spectroscopic investigation. Fraction 2 was shown by GC–MS to consist chiefly of chlorinated dehydroabietic acids, together with minor amounts of unidentified materials.

Fraction 4 was a single component by TLC and by GC after methylation. The compound was identified as 9,10-epoxystearic acid by IR, NMR, and mass spectrometry and by synthesis from oleic acid. Chromatographic analyses showed that the same compound was a major constituent of Fractions 3–6 and a minor component in Fraction 7.

Fractions 8–10 were not examined in detail since they were of low toxicity to rainbow trout when tested at 5 times the concentration of material occurring in the original effluent.

The constituents in Fraction 1 could not be separated quantitatively and it was not possible, therefore, to make a solution containing the correct concentrations of isolated materials for toxicity comparison with the original caustic extraction effluent. Instead, GC response factors were determined for the five isolated toxic compounds relative to a methyl pentadecanoate internal standard. Effluent samples from two mills were then passed through XAD-2 resin; the ether–methanol extracts of the adsorbed constituents were methylated and were analyzed quantitatively by GC. The constituents were identified by GC–MS.

Solutions were made containing the toxic compounds in the concentrations found by GC analysis. For each sample there was a close relationship between the bioassay graph of the caustic extraction effluent and that of the corresponding synthetic toxic solution (Fig. 4).

TOXICITIES OF THE ISOLATED COMPOUNDS

The toxicities to rainbow trout of the pure compounds identified in caustic extraction effluent were measured in static bioassays.

Resin acids isolated from pulpmill effluents

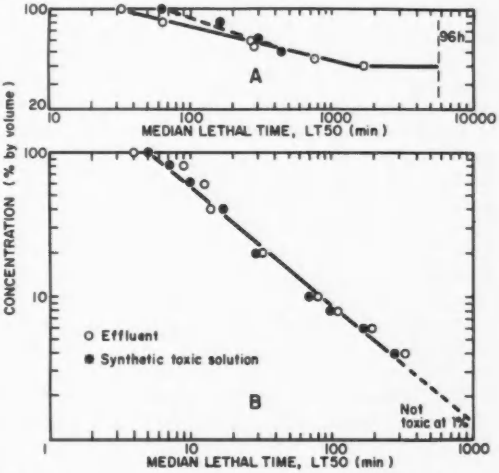


FIG. 4. Concentration–toxicity relationships of two caustic extraction effluents and their synthetic toxic solutions. A, Effluent from Mill I, Table 3; B, effluent from Mill II, Table 3.

TABLE 2. Weights of acidic fractions isolated from 160 liters of caustic extraction effluent, and their toxicities at 5 times the concentrations found in the effluent.

Fraction no.	1	2	3	4	5	6	7	8	9	10
Weight (*mg*)	487	382	605	801	320	498	356	569	725	226
LT50 (*min*) at 5 times effluent concn.	9	117	17	11	51	137	196	1793	1379	>96 h

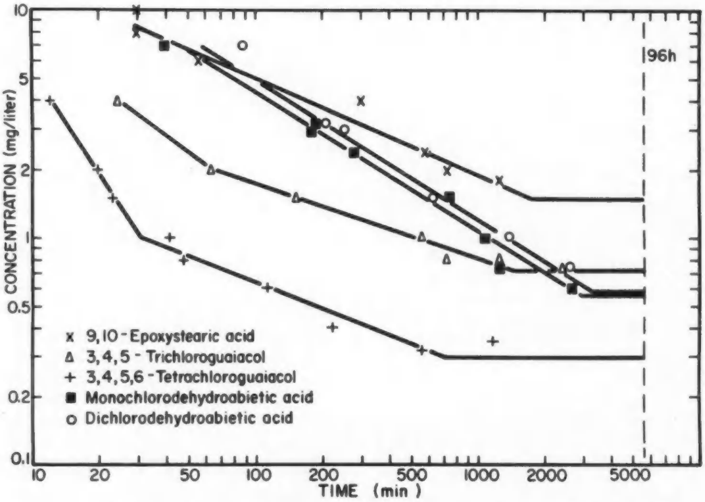


FIG. 5. Concentration–LT50 curves for pure toxicants isolated from caustic extraction effluent.

exhibit a marked increase in toxicity with decreasing pH in the range pH 7.5–6.4, indicating that the un-ionized forms of these acids are more toxic than the corresponding sodium salts (Leach and Thakore 1974a). Since the toxic compounds isolated from caustic extraction effluent are also weak acids, bioassays were carried out in solutions buffered at pH 6.4.

Median lethal times (LT50) at various concentrations are shown in Fig. 5; 96-h median lethal concentrations (LC50) were measured from the log-probit plots of Fig. 6 (American Public Health Association, American Water Works Association, and Water Pollution Control Federation 1971). Dehydroabietic acid, tested as a reference toxicant (Davis and Hoos 1974), had a 96-h LC50 of 1.1 mg/liter under the same bioassay conditions.

The most toxic compound was tetrachloroguaiacol, which had a 96-h LC50 of 0.32 mg/liter, less than half that of trichloroguaiacol (0.75 mg/liter). Both chlorinated dehydroabietic acids had 96-h LC50's of approximately 0.6 mg/liter. At low concentrations, 9,10-epoxystearic acid was the least toxic of the compounds isolated, but its toxicity increased more rapidly with concentration than did the toxicities of the chlorinated dehydroabietic acids.

Caustic extraction effluents from six western Canada kraft mills were analyzed by GC for the five toxicants isolated in this study. Full details of the analytical procedure will be given in a future publication. A GC trace obtained using a SILAR-10C GC column is shown in Fig. 7. The baseline drift is due to breakdown products from 9,10-epoxystearic acid, which is unstable on this stationary phase. Levels of 9,10-epoxystearic acid were measured separately using an SE-30 GC column. Trichloro- and tetrachloro-veratroles (Fig. 7) were formed by methylation of the corresponding guaiacols. The concentrations of toxicants found in the caustic extraction effluents are listed in Table 3. In most samples, levels of individual toxic compounds were higher than their 96-h

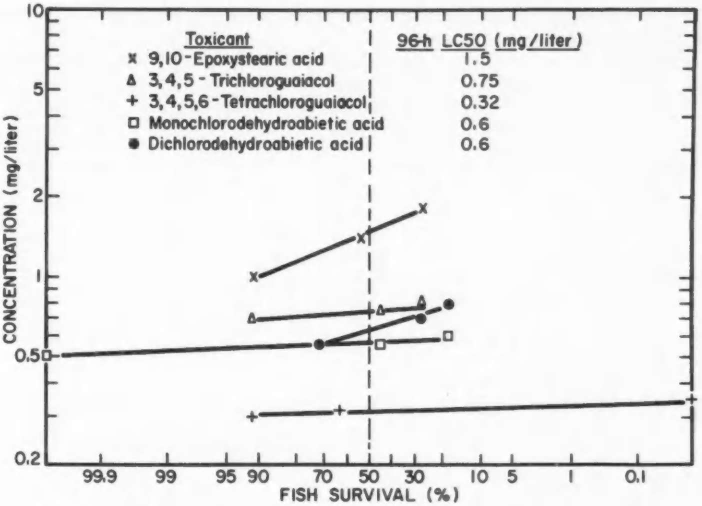


FIG. 6. 96-h median lethal concentrations of pure toxicants isolated from caustic extraction effluent.

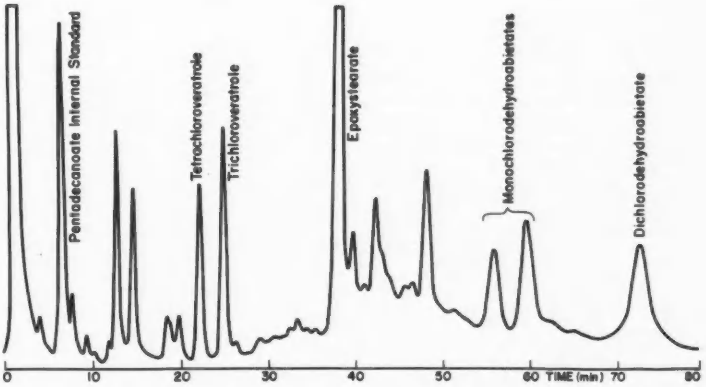


FIG. 7. GC trace of methylated toxic extract from caustic extraction effluent. Column: 6 ft × ⅛ in SS containing 10% SILAR-10 C on 100–120 mesh Gas Chrom P. He flowrate 12 ml/min. Temperature: 5 min at 150 C then 2 C/min to 220 C. Instrument: Perkin-Elmer 881; attenuation 50.

LC50's. Toxicant concentrations were converted to rainbow trout toxic units using the concept summarized by Sprague and Ramsay (1965), Sprague (1970), and Brown (1968). The sum of toxic units in each sample was considerably greater than the lethal threshold value of 1 TU.

Discussion

The bioassay and chemical analysis data, after conversion to toxic units, indicate that the five compounds isolated in this study are important toxic constituents in caustic extraction effluents from kraft mills operating on western softwoods. Other toxic constituents were undoubtedly not identified, e.g., in the nonacidic fraction of the effluent, but they are likely to be of relatively minor importance compared with the types of toxicants that were characterized. Although acidic Fractions 1 and 4 (Fig. 1) were the only ones separated into pure constituents, the compounds isolated from them are believed to account for

Table 3. Concentrations of toxic materials (milligrams per liter) and the sums of toxic units in caustic extraction effluent samples. ND = not detected.

Mill code	Trichloro-guaiacol	Tetrachloro-guaiacol	Monochloro-dehydroabietic acid	Dichloro-dehydroabietic acid	Epoxy-stearic acid	Rainbow trout TU (*total*)
I	0.6	0.5	ND	ND	2.1	3.7
I	0.4	0.3	ND	ND	2.0	2.7
II	1.1	1.1	4.3	2.5	4.7	19
II	0.8	0.6	3.4	2.1	17	24
III	0.4	0.3	0.4	0.7	6.0	7.5
IV	0.3	0.3	ND	ND	1.5	2.3
V	0.8	0.6	0.2	0.2	2.1	4.7
VI	0.7	0.7	0.9	1.8	4.9	10.8
96-h LC50	0.75	0.32	0.6	0.6	1.5	—

most of the toxicity of the other acidic fractions, based on GC–MS and bioassay evidence. Thus, toxicity in Fraction 2 is probably due to the presence of chlorinated dehydroabietic acids, and epoxystearic acid is believed to be responsible for most of the toxicity of Fractions 3, 5, 6, and 7. Work is continuing in attempts to identify the other toxic factors in caustic extraction effluents from a variety of mills.

Concentrations of toxic materials and, to some extent, the types of toxic compounds in caustic extraction effluents will depend on mill operating conditions. Water-use per ton of pulp and the amount and type of water recycled in a bleach plant will affect the concentrations of all toxicants. Amounts of chlorinated guaiacols, which are derived from lignin cleavage reactions (Dence 1971), may be additionally influenced by the kappa number (lignin content) of the unbleached pulp.

Resin acids are major toxic constituents in softwood kraft pulping effluent (unbleached whitewater; Leach and Thakore 1973, 1974a). If the brownstock pulp is not washed free of unbleached whitewater, resin acids will be carried with the pulp into the bleach plant and may be chlorinated in the first stage of bleaching. GC analyses of 17 samples of caustic extraction effluent from seven mills showed that concentrations of unchlorinated resin acids were normally less than 1 mg/liter (Leach and Thakore 1974b). A few samples contained up to 5 mg/liter. In one sample the concentration of unchlorinated resin acids was 11 mg/liter due to abnormal operation of the brownstock washers. Even in this sample, unchlorinated resin acids accounted for only 30% of the effluent toxicity. Only the more stable resin acids survive the strong oxidizing conditions of the first chlorination stage. Consequently, dehydroabietic acid and its chlorinated derivatives are the predominant resin acids in caustic extraction effluents.

Epoxystearic acid may result from hypochlorination of oleic acid in the first stage of the bleaching sequence, followed by dehydrochlorination to give an epoxide in the caustic extraction stage. The concentrations of epoxystearic acid encountered in the effluents analyzed are very high relative to other fatty acids and it is possible that this compound may be formed by reactions of bleaching chemicals with an oleic acid derivative in a process additive, such as a pitch dispersant or a defoamer.

There was no indication of the presence in caustic extraction effluent of tetrachloro-*o*-benzoquinone, found by Das et al. (1969) in chlorination stage effluent, nor of the chlorocatechols tested by Servizi et al. (1968) as possible toxicants in bleachery effluents. However, the chlorinated guaiacols identified in this study are structurally very similar to chlorinated catechols.

All the chlorinated constituents isolated from caustic extraction effluent are more toxic to rainbow trout in static bioassays than are resin acids (Leach and Thakore 1973). Differences were small between acutely toxic and nontoxic concentrations of chlorinated compounds. For instance, in solutions of monochlorodehydroabietic acid, 100% fish mortality occurred by 96 h at a concentration of 0.75 mg/liter, but there were no deaths in a 0.50 mg/liter solution. In tetrachloroguaiacol solutions, all fish survived at 0.30 mg/liter, none were alive after 96 h at 0.35 mg/liter. Similar observations were made for chlorinated catechols by Servizi et al. (1968), who found 96-h LC50's of approximately 0.3 mg/liter for tetrachlorocatechol using pink salmon (*Oncorhynchus gorbuscha*) fry and alevins.

The mechanism of toxic action of epoxystearic acid may parallel that reported by Wildish (1974) for polyoxyethylene ethers, since they have similar chemical structures. Chlorinated phenolics in caustic extraction effluents could interfere with phosphorylation processes in the gill membranes of fish in a manner analogous to that proposed for pentachlorophenol (White et al. 1959).

Biodegradation of chlorinated organic compounds occurs very slowly (Edwards 1974). Thus, the chlorinated phenolics and chlorinated resin acids in caustic extraction effluents may be difficult to eliminate in the bio-treatment systems used by many mills, and these compounds could find their way into receiving waters. Trichloroveratrole has in fact been reported in a methylated extract of aerobically treated bleached kraft whole mill effluent (Rogers 1973). It was presumed to arise from trichloroguaiacol or trichlorocatechol during preparation of the extract.

Acknowledgments

The study was funded by the Canadian Forestry Service, Ottawa through its Co-operative Pollution Abatement Research (CPAR) program, as part of project no. 245. The technical contributions of Messrs L. T. K. Chung and H. P. Meier and the advice of Drs C. C. Walden and T. E. Howard during the investigation are appreciated. GC–MS and NMR facilities were made available by Simon Fraser University Chemistry Department, courtesy of Dr A. C. Oehlschlager, who also provided guidance in the study. Mass spectra were obtained by Mr G. Owens. The cooperation of personnel at several western Canada kraft mills is gratefully acknowledged.

American Public Health Association, American Water Works Association, and Water Pollution Control Federation. 1971. Standard methods for the examination of water and wastewater. 13th ed. New York, N.Y. 874 p.

Anon. 1947. McIlvaine's standard buffer solutions, p. 1405. *In* C.D. Hodgman [ed.] Handbook of chemistry and physics. 30th ed. Chemical Rubber Publishing Company, Cleveland, Ohio.

Aplin, R. T., and L. Coles. 1967. A simple procedure for localisation of ethylenic bonds by mass spectrometry. Chem. Commun. 00: 858–859.

Betts, J. L., and G. G. Wilson. 1966. New methods for reducing the toxicity of kraft mill bleachery wastes to young salmon. J. Fish. Res. Board Can. 23: 813–824.

Brown, V. M. 1968. The calculation of the acute toxicity of mixtures of poisons to rainbow trout. Water Res. 2: 723–733.

Das, B. S., S. G. Reid, J. L. Betts, and K. Patrick. 1969. Tetrachloro-*o*-benzoquinone as a component in bleached kraft chlorination effluent toxic to young salmon. J. Fish. Res. Board Can. 26: 3055–3067.

Davis, J. C., and R. A. W. Hoos. 1974. Use of sodium pentachlorophenate and dehydroabietic acid as reference toxicants for salmonid bioassays — interlaboratory co-operative study. Fish. Mar. Serv. Res. Dev. Tech. Rep. 464: 11 p.

Dence, C. W. 1971. Reactions of lignins. Halogenation and nitration, p. 373–432. *In* K. V. Sarkanen and C. H. Ludwig [ed.] Lignins, occurrence, formation, structure and reactions. John Wiley and Sons, Inc., New York, N.Y.

Edwards, C. A. 1974. Persistent pesticides in the environment. 2nd ed. Chemical Rubber Company Press, Cleveland, Ohio. 170 p.

Heilbron, I., and H. M. Bunbury. [ed.] 1953. Dictionary of organic compounds. Eyre and Spottiswoode, London. 4: 560 p.

Howard, T. E., and C. C. Walden. 1971. Effluent characteristics of bleached kraft pulp mills. Pulp Pap. Mag. Can. 72: T3–T9.

Leach, J. M., and A. N. Thakore. 1973. Identification of the constituents of kraft pulping effluent that are toxic to juvenile coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 30: 479–484.

1974a. Isolation of the toxic constituents of kraft pulp mill effluents. CPAR Rep. 11-4. Canadian Forestry Service, Ottawa, Ont.

1974b. Identification of the toxic constituents in kraft mill bleach plant effluents. CPAR Rep. 245-1. Canadian Forestry Service, Ottawa, Ont.

Rogers, I. H. 1973. Isolation and chemical identification of toxic components of kraft mill wastes. Pulp Pap. Mag. Can. 74: T303–T308.

Ryhage, R., and E. Stenhagen. 1960. Mass spectrometric studies. VI. Methyl esters of normal chain oxo-, hydroxy-, methoxy- and epoxy-acids. Ark. Kemi. 15: 545–574.

Sarkanen, K. V., and C. W. Dence. 1960. Reactions of *p*-hydroxybenzyl alcohol derivatives and their methyl ethers with molecular chlorine. J. Org. Chem. 25: 715–720.

Servizi, J. A., R. W. Gordon, and D. W. Martens. 1968. Toxicity of two chlorinated catechols, possible components of kraft pulp mill bleach waste. Int. Pac. Salmon Fish. Comm. Prog. Rep. 17: 43 p.

Sprague, J. B. 1970. Measurement of pollutant toxicity to fish. II. Utilizing and applying bioassay results. Water Res. 4: 3–32.

Sprague, J. B., and B. A. Ramsay. 1965. Lethal levels of mixed copper–zinc solutions for juvenile salmon. J. Fish. Res. Board Can. 22: 425–432.

White, A., P. Handler, E. L. Smith, and D. Stetten Jr. 1959. Principles of biochemistry. 2nd ed. McGraw-Hill, Inc., New York, N.Y. 1162 p.

Wildish, D. J. 1974. Lethal response by Atlantic salmon parr to some polyoxyethylated cationic and nonionic surfactants. Water Res. 8: 433–437.

Witnauer, L. P., and D. Swern. 1950. X-ray diffraction and melting-point composition studies on the 9,10-epoxy- and dihydroxystearic acids and 9,10-epoxyoctadecanols. J. Am. Chem. Soc. 72: 3364–3368.

Passage of Fish Eggs and Young Through a Pumped Storage Generating Station[1]

DARREL E. SNYDER[2]

Ichthyological Associates, Drumore, Pa. 17518, USA

SNYDER, D. E. 1975. Passage of fish eggs and young through a pumped storage generating station. J. Fish. Res. Board Can. 32: 1259–1266.

During June and July 1970, an estimated 5.3 million eggs (4.1/10^{3}m^3) and 56.6 million young fish (43.8/10^{3}m^3), 3–62 mm FL, were pumped by the Muddy Run Pumped Storage Generating Station from Conowingo Reservoir (lower Susquehanna River, Pennsylvania) into Muddy Run Pumped Storage Reservoir. A maximum of only 2% of the eggs and 39% of the young were returned to the lower reservoir during generation. The eggs were predominately *Carpiodes cyprinus*. Of the young, 73% entrained during pumping and 83% entrained during generating were *Ictalurus punctatus*, *Cyprinus carpio*, and *Carpiodes cyprinus*. Similar results are reported for 1969. The species and numbers of specimens entrained reflect the utilization of the area near and above the lower reservoir intake discharge structure as spawning and nursery grounds, the extent and peaks of spawning seasons, and the phases of development and behavior of the young. Sufficient numbers of specimens pumped into and retained by the upper reservoir, in which natural reproduction is nearly precluded by the extensive fluctuation of water level, survive to maintain many of the reservoir's fish populations.

SNYDER, D. E. 1975. Passage of fish eggs and young through a pumped storage generating station. J. Fish. Res. Board Can. 32: 1259–1266.

En juin et juillet 1970, des nombres estimés à 5.3 millions (4.1/10^{3}m^3) d'œufs et 56.6 millions de jeunes poissons (43.8/10^{3}m^3) de 3 à 62 mm de LF ont été pompés du réservoir Conowingo (basse Susquehanna, Pennsylvanie) dans le réservoir d'entreposage Muddy Run par la centrale hydro-électrique de Muddy Run. Tout au plus, seulement 2% des œufs et 39% des jeunes furent retournés au réservoir inférieur pendant la génération d'électricité. Les œufs étaient en grande partie des œufs de *Carpiodes cyprinus*. Parmi les jeunes, 73% entraînés lors du pompage et 83% entraînés lors de la génération étaient *Ictalurus punctatus*, *Cyprinus carpio* et *Carpiodes cyprinus*. On a rapporté des résultats semblables en 1969. Les espèces et le nombre de spécimens entraînés reflètent l'utilisation de l'aire dans le voisinage et en amont de l'installation de prise d'eau et de décharge du réservoir inférieur comme frayères et lieux d'alevinage, l'étendue et les pics des saisons de fraie et les diverses phases de développement et de comportement des jeunes. Un nombre suffisant de spécimens pompés et retenus dans le réservoir supérieur, où les fluctuations considérables du niveau d'eau empêchent presque complètement la reproduction naturelle, survivent pour maintenir plusieurs des populations de poissons du réservoir.

Received August 6, 1974
Accepted March 13, 1975

Reçu le 6 août 1974
Accepté le 13 mar 1975

PUMPED storage generating facilities pump water into an elevated reservoir when electrical demand is low and excess electricity is available. When electrical demand is high the water is returned to a lower reservoir via generation. Such facilities are relatively new to the power industry, e.g. 22 have been constructed thus far in the United States, and much remains to be learned about their biological impact. Detailed studies of the extent and survival of fish passing through these generating stations and the subsequent effects on the existing and newly created ecosystems must be evaluated. This study was undertaken to determine the species, numbers, and periods of vulnerability of fish eggs and young (young-of-the-year) fishes entrained during the pumping and generating operations of the 800-MW Muddy Run Pumped Storage Generating Station (Muddy Run Station).

The Study Area

The study area includes the Conowingo Reservoir, an impoundment on the lower Susquehanna River, Pennsylvania; the Muddy Run Reservoir, constructed

---

[1] Based on a portion of the author's Master's Thesis (Snyder 1971).

[2] Present address: Ecological Sciences Div., NUS Corp., Ecological Sciences Center, 2419 Baldwick Road, Pittsburgh, Pa. 15205, USA.

Printed in Canada (J3510)
Imprimé au Canada (J3510)

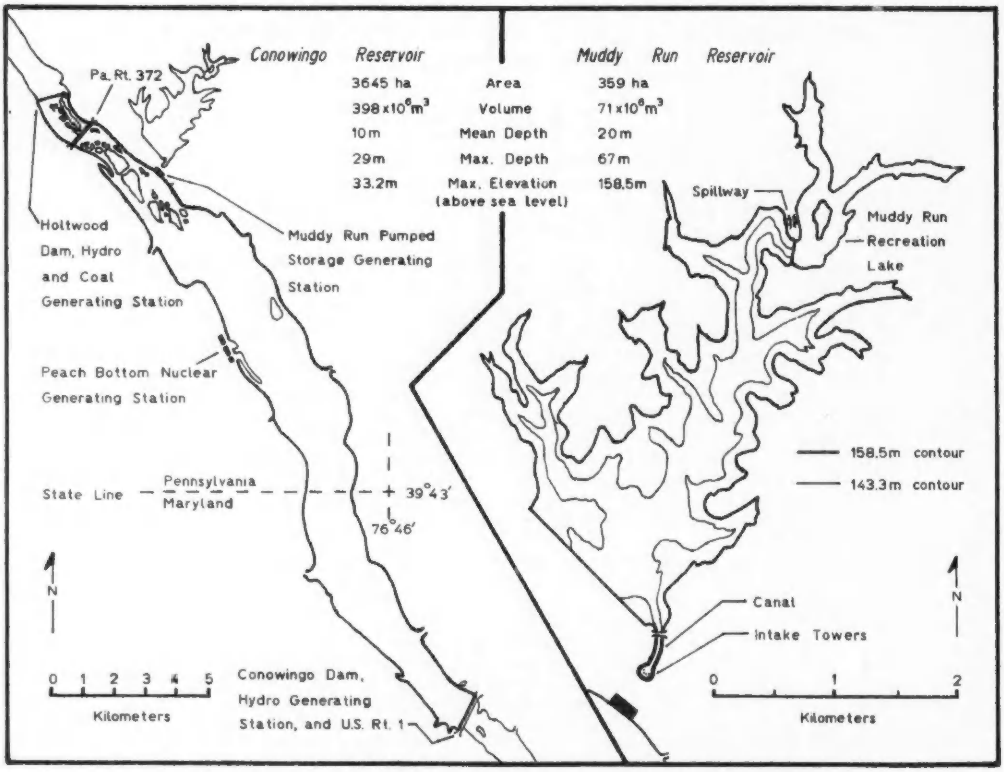

Conowingo Reservoir
Muddy Run Reservoir
3645 ha Area 359 ha
398x10⁶m³ Volume 71x10⁶m³
10m Mean Depth 20m
29m Max. Depth 67m
33.2m Max. Elevation (above sea level) 158.5m
Pa. Rt. 372
Holtwood Dam, Hydro and Coal Generating Station
Muddy Run Pumped Storage Generating Station
Peach Bottom Nuclear Generating Station
State Line
Pennsylvania
Maryland
39°43′
76°46′
N
0 1 2 3 4 5
Kilometers
Conowingo Dam, Hydro Generating Station, and U.S. Rt. 1
Spillway
Muddy Run Recreation Lake
158.5m contour
143.3m contour
Canal
Intake Towers
N
0 1 2
Kilometers

FIG. 1. Conowingo Reservoir (Susquehanna River) and Muddy Run (Pumped Storage) Reservoir.

125 m (maximum water level) above Conowingo Reservoir; and a 700 m long canal (base width of 56 m and maximum depth of 24 m) connecting the upper intake discharge towers of the Muddy Run Station with the Muddy Run Reservoir (Fig. 1). All water transported between the two reservoirs passes through this canal. The Muddy Run Reservoir was first filled to capacity in late June 1967, three months after the power station had begun limited operation. All eight reversible pump-turbines, with a combined pumping capacity of 738.6 m^3/s and generating capacity of 877.3 m^3/s, were operational by February 1968. Based on the days of sampling, an average of $28.7 \times 10^6 m^3$ of water (7.2% of the volume of Conowingo Reservoir) passed through the station into the Muddy Run Reservoir during each pumping operation and back into the Conowingo Reservoir during each generating operation during June and July 1970 (Snyder 1971). Normally, the water in Muddy Run Reservoir is drawn down during generation on weekdays, partially refilled by pumping at night, and completely refilled on weekends. Maximum drawdown, representing 55% of the reservoir's capacity, is about 15.2 m which can occur in approximately 15 h. Water is also contributed to Muddy Run Reservoir by several small streams and springs, and by the adjacent 40.5-ha Muddy Run Recreation Lake via a spillway. The lake was constructed and originally filled concurrently with Muddy Run Reservoir. Topping et al. (1970) and Robbins and Mathur (1974) described the limnological conditions of both reservoirs and the lake.

Fishes of the Area

Raney and Robbins (1969), Robbins et al. (1970), and Robbins and Mathur (1974), reported on the fishery aspects of the area. Fifty-three species were reported in the Conowingo Reservoir and its tributary streams. The major species, in decreasing order of numerical abundance, were the white crappie (*Pomoxis annularis*), channel catfish (*Ictalurus punctatus*), bluegill (*Lepomis macrochirus*), and spotfin shiner (*Notropis spilopterus*). However, seine, trawl, trapnet, and meternet collections also indicated abundant populations of carp (*Cyprinus carpio*), spottail shiner (*Notropis hudsonius*), bluntnose minnow (*Pimephales notatus*), quillback (*Carpiodes cyprinus*), pumpkinseed (*Lepomis gibbosus*), and tessellated darter (*Etheostoma olmstedi*). The reservoir is stocked annually with walleye (*Stizostedion vitreum vitreum*) larvae and the tributaries are stocked each spring with brook, brown, and rainbow trout (*Salvelinus fontinalis, Salmo trutta,* and *Salmo gairdneri*). Anadromous fishes have been transported over the Conowingo Dam at various times as part of an American shad (*Alosa sapidissima*) restoration program.

Most fishes common to Conowingo Reservoir are now found in Muddy Run Reservoir; 40 species have been reported. The major species, in decreasing order of numerical abundance were carp, channel catfish, quillback, and white crappie. Notable populations of spotfin shiner, bluegill, tessellated darter, and smallmouth bass (*Micropterus dolomieui*) were also reported. The extensive fluctuation of water level in Muddy Run Reservoir severely restricts successful spawning. However, it is possible that in the spring of 1967 when water level fluctuation was limited, adults of some species pumped from Conowingo Reservoir may have reproduced in Muddy Run Reservoir. Since that time, only one possibly viable spawning site has been located in the reservoir — a rock ledge where pools of water are retained when the reservoir level drops below it. Nests of the pumpkinseed have been observed there (Snyder 1971).

Thirty-two species have been reported in the Recreation Lake; the abundant species were the bluegill, pumpkinseed, and white crappie. Brook trout and northern pike (*Esox lucius*) have been stocked in the lake.

Methods

On a weekly schedule, when possible, for most of the spawning seasons of 1969 and 1970, a series of successive 0.5-h collections were taken during pumping and either the preceding or following generating phase of station operation. Samples were collected with a pair of stationary 1-m conical plankton nets (0.4 × 0.6 mm mesh) tied to a bridge support column in the middle of the northern portion of the upper reservoir intake–discharge canal. The nets were sampled simultaneously, one at the surface and the other at the bottom. Exceptions were that only surface samples were taken from late May through June 1969 and during pumping in early June 1970. Only bottom samples were taken in early July 1969.

Samples were initially preserved in 5–10% formalin solution with Rose Bengal dye usually added to facilitate sorting. Fish were identified and counted, and most were measured to the nearest millimeter, fork length. The bases for species identification and an original family key for larval fishes are given by Snyder (1971).

The volume of water filtered for each sample was estimated by multiplying the area of the mouth of the net by the mean velocity of water flowing through the northern portion of the canal during the specific sampling period. Mean velocity at any particular moment was calculated by dividing the amount of water (m^3/s) passing through the station (data provided by the Philadelphia Electric Company) by the cross-sectional area (m^2) of the water in the canal (based on knowledge of the shape and dimensions of the canal and the canal water level during each sampling period). The average sample collected during this study was taken in a mean flow of 81 cm/s and is estimated to have filtered 1145 m^3 of water. Since the actual velocity of water sampled by nets at the surface and bottom was probably less than the mean velocity in the canal, and since plankton net filtration efficiency was certainly less than 100% (Dovel 1964), the densities of specimens reported herein are considered conservative.

Results

A total of 1513 eggs, 6309 young, and 39 yearling or older fish were taken in 249 samples collected from late May through mid-August 1969 and June through July 1970. Twenty-three species representing five families were identified (Table 1). The eggs collected were predominately quillback, though a few were carp. Of the identifiable young, 98% were identified to species (10% of all young were "unidentifiable" due to damage or deterioration). Channel catfish, carp, quillback, tessellated darter, spotfin shiner, and bluegill accounted for 96% of the young identified to species. Although the size range of young fish collected varied from 3 to 62 mm FL, most were in some phase of larval development. Fifty-three percent measured less than 15 mm, 82% less than 20 mm, and 94% less than 30 mm. The yearling and older fish collected were predominately channel catfish (82%); the others were spottail shiner, spotfin shiner, bluegill, and white crappie.

Based on mean numbers collected in each third of a month, in June and July 1970 a mean of 4.1 eggs per 10^3m^3 was taken during pumping but only 0.1 per 10^3m^3 during generating (Table 1). Of the eggs collected during pumping, 90% were taken in early June (Table 2). With the exception of early June when no bottom pumping samples were taken, 79% of the eggs in pumping samples were collected at the bottom. The eggs in generating samples were taken only in mid-June at the surface and late June at the bottom.

During the same period, a mean of 43.8 young fish per 10^3m^3 were collected during pumping, but only 16.9 per 10^3m^3 during generating (Table 1). Of the young collected, channel catfish, carp, and quillback accounted for 35, 20, and 19%, respectively, during pumping; and 42, 32, and 10%, respectively, during generating. Of the young collected during pumping, 21–23% were taken in each, early June, late June and in mid-July, 8% in mid-June, 4% in early July, and 3% in late July. Excluding the pumping samples of early June, more fish were collected at the bottom than

TABLE 1. Mean numbers[a] of fish eggs and young per 10^{3}m^3 collected by stationary 1-m plankton nets in Muddy Run Reservoir Canal during pumping and generating operations in late May through July and mid-August 1969 and June through July 1970. Percentage composition given in parentheses.

	1969		1970	
Species	Pumping	Generating	Pumping	Generating
Eggs	53.33	—	4.10	0.10
Young				
Cyprinus carpio	10.23 (27.5)	1.08 (21.2)	8.58 (19.6)	1.62 (9.6)
Exoglossum maxillingua	—	—	0.02 (0.0)	—
Nocomis micropogon	—	—	0.01 (0.0)	—
Notemigonus crysoleucas	—	—	—	0.01 (0.1)
Notropis amoenus	—	—	0.02 (0.0)	0.01 (0.1)
Notropis hudsonius	0.12 (0.3)	0.02 (0.4)	0.26 (0.6)	0.05 (0.3)
Notropis spilopterus	0.42 (1.1)	0.15 (2.9)	0.76 (1.7)	0.31 (1.8)
Pimephales notatus	0.01 (0.0)	—	0.05 (0.1)	0.03 (0.2)
Cyprinidae, unidentified	0.11 (0.3)	0.04 (0.8)	0.97 (2.2)	0.15 (0.9)
Carpiodes cyprinus	5.33 (14.4)	1.37 (26.9)	8.25 (18.8)	5.42 (32.0)
Catostomus commersoni	—	—	0.29 (0.7)	0.02 (0.1)
Erimyzon oblongus	—	—	0.02 (0.0)	—
Hypentelium nigricans	0.15 (0.4)	—	0.01 (0.0)	—
Ictalurus natalis	0.11 (0.3)	—	0.27 (0.6)	—
Ictalurus punctatus	9.00 (24.2)	1.77 (34.8)	15.18 (34.6)	7.09 (41.9)
Noturus insignis	0.02 (0.1)	—	0.01 (0.0)	—
Ambloplites rupestris	0.16 (0.4)	0.01 (0.2)	0.08 (0.2)	0.01 (0.1)
Lepomis auritus	0.01 (0.0)	—	—	—
Lepomis gibbosus	0.07 (0.2)	0.04 (0.8)	0.06 (0.1)	0.04 (0.2)
Lepomis macrochirus	0.16 (0.4)	0.12 (2.4)	0.64 (1.5)	0.65 (3.8)
Micropterus dolomieui	0.33 (0.9)	—	0.12 (0.3)	0.05 (0.3)
Pomoxis annularis	0.11 (0.3)	0.03 (0.6)	0.23 (0.5)	0.26 (1.5)
Etheostoma olmstedi	3.31 (8.9)	0.19 (3.7)	1.25 (2.9)	0.50 (3.0)
Percina peltata	0.14 (0.4)	—	0.04 (0.1)	0.03 (0.2)
Unidentifiable	7.35 (19.8)	0.27 (5.3)	6.71 (15.3)	0.67 (4.0)
Total young	37.14	5.09	43.83	16.92
Number of 0.5-h samples (surface–bottom)	43–25	44–28	29–29	30–27

[a]Calculated by averaging the means of surface and bottom samples for each third of a month, except when only surface or only bottom samples were taken, then averaging these values for the year.

the surface, i.e. 64% during pumping and 84% during generating.

The June and July collections of 1969 provide somewhat similar results, although only surface collections were taken in June and only bottom collections in early July (Tables 1 and 3). Means of 9.8 eggs and 33.5 young fish per 10^{3}m^3 were pumped from Conowingo Reservoir in June and July, while only 4.5 young per 10^{3}m^3 were entrained during generating. The surface collections of late May provided 367.8 eggs per 10^{3}m^3 during pumping but none during generating. They also yielded 95.2 young fish per 10^{3}m^3 during pumping but only 12.6 per 10^{3}m^3 during generating. Half of the young in the pumping collections of late May were unidentifiable; among the identifiable, 57% were quillback, 31% carp, and 8% tessellated darter. In the generating samples of late May, quillback accounted for 84% of the young collected. The mid-August collections yielded no eggs and few young fish, less than 1.0 per 10^{3}m^3. Channel catfish and spotfin shiner accounted for 75 and 8%, respectively, of the young fish collected in mid-August during pumping, and 65 and 27%, respectively, of those collected during generating.

Discussion and Conclusions

During June and July 1970, an estimated 5.3 million eggs and 56.6 million young fish were pumped from Conowingo Reservoir through the Muddy Run Station into Muddy Run Reservoir (4.1 eggs and 43.8 young/10^{3}m^3; 28.7 × 10^{6}m^3/average pumping operations; 5 pumping operations/week; 9 wk in June and July). The corresponding estimates based on the less complete sampling of 1969 were 12.7 million eggs and 43.3

TABLE 2. Numbers of fish eggs and young per $10^3 m^3$ collected by stationary 1-m plankton nets at the surface (S) and bottom (B) of Muddy Run Reservoir Canal during pumping (P) and generating (G) operations in 1970.

		June			July		
		Early	Mid	Late	Early	Mid	Late
		S / B	S / B	S / B	S / B	S/ B	S / B
	P	1 / -	3 / 4	5 / 5	5 / 5	5 / 5	10 / 10
No. 0.5-h samples	G	5 / 3	5 / 4	5 / 5	5 / 5	5 / 5	5 / 5
Eggs							
Total	P	22.15/	— / 0.21	0.85/ 1.92	— / —	0.17/ 1.02	— /0.64
eggs	G	— / —	0.94/ —	— / 0.13	— / —	— / —	— / —
Young							
Ictalurus	P	— /	10.90/22.99	22.17/34.71	9.50/34.94	9.36/29.56	2.02/4.24
punctatus	G	— / —	1.42/ 0.21	— /30.15	— / 2.99	0.77/44.21	— /5.20
Cyprinus	P	1.59/	16.75/20.34	10.65/ 6.50	1.27/ 1.17	11.64/30.46	0.40/0.08
carpio	G	3.06/ 0.53	2.41/ 1.53	1.05/ 2.44	0.22/ 0.52	2.66/ 4.25	— / —
Carpiodes	P	38.96/	2.90/ 5.52	2.99/ 8.23	— / 0.18	0.20/ 0.35	— /0.32
cyprinus	G	4.03/72.65	0.70/ 2.28	0.33/ 2.02	— / —	— / 0.35	— / —
Etheostoma	P	1.59/	1.92/ 4.28	1.27/ 1.19	0.38/ 0.40	1.29/ 0.50	0.24/ —
olmstedi	G	— / 1.59	0.74/ 2.84	— / 0.72	— / 0.25	— / 0.54	— / —
Notropis	P	— /	0.75/ 0.56	0.89/ 1.24	— / 0.40	1.62/ 2.86	0.58/0.27
spilopterus	G	0.65/ 0.25	0.10/ —	0.27/ 0.55	0.79/ 0.20	0.33/ 0.35	— /0.17
Lepomis	P	— /	0.47/ 0.88	1.05/ 0.90	0.42/ 1.12	0.22/ 2.32	0.18/ —
macrochirus	G	— / 0.25	0.10/ —	3.70/ 0.12	3.09/ 0.25	— / 0.17	0.17/ —
Other	P	18.48/	11.90/15.40	9.91/ 8.06	0.65/ 2.22	6.91/14.73	1.06/1.63
young	G	4.38/ 1.31	2.46/ 2.28	0.57/ 1.25	0.37/ 0.25	1.10/ 0.52	— /0.54
Total	P	60.62/	45.59/69.97	48.93/60.83	12.22/40.43	31.24/80.78	4.48/6.54
young	G	12.12/76.58	7.93/ 9.14	5.92/37.25	4.47/ 4.46	4.86/50.39	0.17/5.91

TABLE 3. Numbers of fish eggs and young per $10^3 m^3$ collected by stationary 1-m plankton nets at the surface (S) and bottom (B) of Muddy Run Reservoir Canal during pumping (P) and generating (G) operations in 1969.

		May	June			July			August
		Late	Early	Mid	Late	Early	Mid	Late	Mid
		S	S	S	S	B	S / B	S / B	S / B
	P	4[a]	2	4	9	1	10 / 10	8 / 8	6 / 6
No. 0.5-h samples	G	4[b]	2[c]	4	10	4	9 / 9	9 / 9	6 / 6
Eggs									
Total	P	367.84	2.34	56.49	—	—	— / —	— / —	— / —
eggs	G	—	—	—	—	—	— / —	— / —	— / —
Young									
Cyprinus	P	15.05	59.02	7.17	0.22	—	— / 0.06	0.25/ 0.52	— / —
carpio	G	0.67	4.85	0.94	1.17	—	— / —	1.61/ 0.27	0.15/ —
Ictalurus	P	—	—	19.12	11.50	—	12.86/46.36	7.14/15.15	0.32/0.96
punctatus	G	—	—	—	0.07	0.75	— /14.22	— /11.21	— /1.30
Carpiodes	P	27.25	9.20	6.10	0.09	—	— / —	— / —	— / —
cyprinus	G	10.58	—	0.25	0.16	—	— / —	— / —	— / —
Etheostoma	P	4.01	3.34	12.31	4.44	—	1.10/ 2.32	0.84/ 0.56	— / —
olmstedi	G	0.67	—	—	—	0.59	— / 0.22	— / 0.24	— / —
Notropis	P	0.33	0.08	0.69	0.15	—	0.23/ —	1.76/ 2.02	0.14/ —
spilopterus	G	—	—	—	0.20	—	— / 0.09	0.90/ 0.50	— /0.53
Lepomis	P	—	0.08	0.15	0.15	—	0.29/ 0.54	0.91/ 0.11	— / —
macrochirus	G	—	—	—	0.28	—	— / —	1.43/ —	— / —
Other	P	48.57	8.78	7.50	2.05	—	0.37/ 0.89	1.75/ 1.85	0.20/0.08
young	G	0.67	—	0.46	0.36	0.25	— / 1.54	1.14/ 0.43	— / —
Total	P	95.21	80.50	53.04	18.60	—	14.85/50.17	12.65/20.21	0.66/1.04
young	G	12.59	4.85	1.65	2.24	1.59	— /16.07	5.08/12.65	0.15/1.83

[a] Collected as one sample of 2-h duration.
[b] Collected as two samples, each of 1-h duration.
[c] Collected as one sample of 1-h duration.

million young. The inclusion of late May and mid-August data raises these 1969 figures to 91.8 million eggs and 64.0 million young (12 wk).

Most of the eggs and young probably originated in the upper portion of Conowingo Reservoir. However, some may have originated in the river above Holtwood Dam. Others, through relatively few due to the general downstream flow of Conowingo Reservoir, may have been previously transported from Muddy Run Reservoir via generation.

The numbers of eggs and young fishes entrained during pumping are indicative of the utilization of the area near and above the station as spawning and nursery grounds. The importance of this area relative to the rest of Conowingo Reservoir remains undetermined for most species. However, the predominate fishes entrained after mid-May are known to also spawn extensively in other portions of the reservoir or its tributaries. The white crappie, one of the more abundant game fishes in Conowingo Reservoir, accounted for only 0.5% of the young entrained during pumping; thus the area near and above the station can be considered relatively unimportant as a spawning or nursery grounds for this species.

Estimates of the percentages of eggs and young of Conowingo Reservoir fishes entrained by the Muddy Run Station during pumping must await determinations of their distributions and densities in the reservoir. Carlson and McCann (1969) estimated that less than 0.7% of the eggs and 2.9% of the larvae of striped bass (*Morone saxatilis*) produced within the Hudson River Estuary would be vulnerable to removal by the proposed pumped storage station at Cornwall, New York.

The specific periods of vulnerability (Tables 2 and 3) reflect the phases of development and behavior of the young as well as the extent and peaks of spawning seasons. Young channel catfish are most vulnerable from mid-June through July. Carp are most vulnerable in early and mid-June, though as in 1970, they may again be highly susceptible in mid-July. Quillback eggs and young are most vulnerable in late May and early June, perhaps earlier, but they are seldom entrained after June. Tessellated darters are susceptible from late May through June with a peak in mid-June. Data for determining the periods of vulnerability for species collected in fewer numbers are provided by Snyder (1971). The eggs or young of fishes that spawn prior to late May, e.g. yellow perch (*Perca flavescens*) and walleye, may also be vulnerable to pumping entrainment.

If, in the future, entrainment by Muddy Run Station pumping operations is shown to have an undesirable impact on any of Conowingo Reservoir's fishes, the impact could be reduced or eliminated by limiting or curtailing operation during the weeks that the eggs or young of the affected species are most vulnerable. Since the young of some species are believed to congregate near the bottom or in protected areas during daylight and might then be less susceptible to entrainment, potential impact on these species might be reduced by limiting pumping operations to the daylight hours when excess electricity is available (mostly on weekends).

During June and July 1970, an estimated 0.1 million eggs and 21.9 million young fish were entrained by the Muddy Run Station during generating. The corresponding estimate for young fish based on the less complete data of 1969 is 5.9 million (no eggs). The inclusion of late May and mid-August data raises the 1969 figure to 8.8 million young fish.

Since natural reproduction in Muddy Run Reservoir is severely restricted by extensive water level fluctuation, most of these eggs and young are hypothesized to have been previously transported to the reservoir during pumping. Some, however, may have originated in the adjacent Recreation Lake or in the very small tributaries to the reservoir.

Of the eggs and young fish pumped from Conowingo Reservoir, few are again entrained during generating, e.g. a maximum of 2% of the eggs and 39% of the young during June and July 1970. Some of those pumped into Muddy Run Reservoir may be consumed by predators. Unconsumed eggs and dead young may settle to the bottom. Surviving young may move beyond the influence of the strong currents of the intake–discharge canal.

The passage of fish eggs and young into Muddy Run Reservoir during pumping is a major source of recruitment for many reservoir fishes, particularly channel catfish, carp, quillback, and tessellated darter. However, passage of young over the spillway from the Recreation Lake may be a major source for other Muddy Run Reservoir fishes, particularly bluegill (Snyder 1971) and white crappie. A minimum of 37.4 million and 34.7 million young fish were pumped into and retained in Muddy Run Reservoir during June and July of 1969 and 1970, respectively (Fig. 2). No successful evaluations of entrainment survival were conducted. However, one attempt (D. E. Snyder, unpublished data), based on the separation of living and dead specimens in the laboratory prior to preservation, showed that over 60% of the young channel catfish were alive shortly after being pumped through the station. Sampling with towed 1-m plankton nets and dipnets in

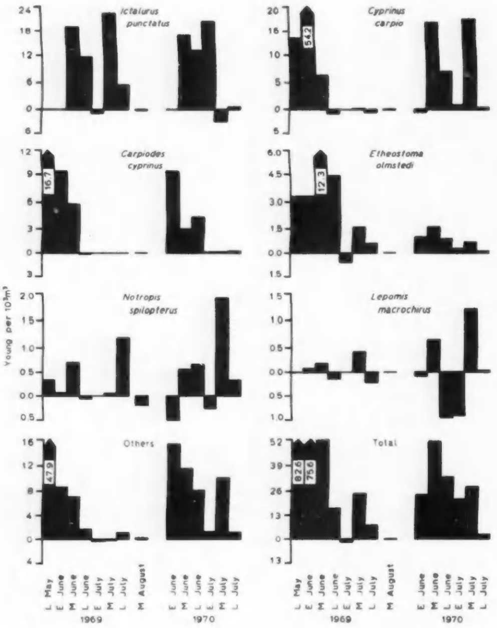


FIG. 2. Mean numbers of young fishes retained in Muddy Run Reservoir with each 10^3m^3 of water pumped by the Muddy Run Station during late (L) May through L July and mid (M)-August 1969, and early (E) June through L July 1970. Numbers below zero represent young removed from Muddy Run Reservoir during generation in excess of those originally pumped into the reservoir.

1968 and 1969 revealed large numbers of living fish larvae in Muddy Run Reservoir (Snyder 1971). In addition, the existence of large populations of several year-classes of channel catfish, carp, and quillback in Muddy Run Reservoir supports the hypothesis that sufficient numbers of eggs and young fish survive entrainment to maintain many of the reservoir's populations.

Acknowledgments

I thank all who had a part in this study and assisted in the production of this paper. P. G. Heisey and J. R. Stauffer developed the sampling techniques and served as field crew. E. Nicodemus served as laboratory assistant. Among many who critically reviewed the manuscript, B. C. Marcy and M. B. Snyder were most influential. The study was part of a research program conducted by Ichthyological Associates (E. C. Raney, director; T. W. Robbins, project leader) for Philadelphia Electric Company. Assistance with publication was provided by Ecological Sciences Division, NUS Corporation.

CARLSON, F. T., AND J. A. MCCANN. 1969. Hudson River fishery investigations, 1965–1968, p. 6–49. *In* A. Jensen [ed.] Evaluations of a proposed pumped storage project at Cornwall, New York in relation to fish in the Hudson River. Report presented to Consolidated Edison Company of New York, Inc., by the Hudson River Policy Committee. 49 p.

DOVEL, W. L. 1964. An approach to sampling estuarine macroplankton. Chesapeake Sci. 5: 77–90.

RANEY, E. C., AND T. W. ROBBINS. 1969. Ecological study of the Conowingo Reservoir, Muddy Run Pumped Storage Reservoir, and the Recreation Lake, 1966–1968, summary and conclusions. Ichthyological Associates, Inc., Drumore, Pa., Misc. Rep. 2: 13 p.

ROBBINS, T. W., AND D. MATHUR. 1974. Preoperational report on the ecology of Conowingo Pond, Peach Bottom Atomic Power Station Units No. 2 and 3. Ichthyological Associates, Inc., Drumore, Pa. Report prepared for Philadelphia Electric Company. 349 p.

ROBBINS, T. W., M. S. TOPPING, AND E. C. RANEY. 1970. Studies of fishes in the Muddy Run Pumped Storage Reservoir and connecting waters, a summary. Ichthyological Associates, Inc., Drumore, Pa., Misc. Rep. 4: 35 p.

SNYDER, D. E. 1971. Studies of larval fishes in Muddy Run Pumped Storage Reservoir near Holtwood, Pennsylvania. M.S. Thesis, Cornell University, Ithaca, N.Y. 212 p.

TOPPING, M. S., H. A. BOYER, AND W. RATZLAFF. 1970. A summary of limnological conditions in Muddy Run Recreation Lake and Muddy Run Pumped Storage Reservoir, 1967–1969. Ichthyological Associates, Inc., Drumore, Pa., Prog. Rep. 7: 42 p.

Fish Viruses — Survival and Inactivation of Infectious Pancreatic Necrosis Virus

R. M. MACKELVIE AND DENISE DESAUTELS

Department of the Environment, Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S. B3J 2R3

MACKELVIE, R. M., AND D. DESAUTELS. 1975. Fish viruses — survival and inactivation of infectious pancreatic necrosis virus. J. Fish. Res. Board Can. 32: 1267–1273.

The survival of infectious pancreatic necrosis (IPN) virus under conditions pertaining to its retention in the laboratory, and its inactivation by several physical and chemical means were examined.

Approximately 99.9% of infectivity was lost when washed IPN virus ($10^{6.5}$–$10^{7.0}$ $TCID_{50}$/ml), suspended in phosphate buffered saline (PBS) and Eagle's Minimal Essential Medium diluted 1:10 with PBS, was held at 4 C for 1 yr. After 2 yr more than 10^2 $TCID_{50}$/ml remained in both suspensions. The virus survived equally well for 1 yr in 20 and 50% glycerol.

Thermal inactivation of IPN virus at 60 C proceeded in a two-component manner, each component following first-order kinetics. At neutral pH, the infectivity of 10^7 $TCID_{50}$/ml was reduced by 99.9% in the first 30 min of exposure. After 5 h, 0.0001% still survived. Inactivation rate of the initial rapid component was increased by adjustment of pH to 3 and 10.

The curve for the 1:4000 formalin inactivation of $10^{6.5}$ $TCID_{50}$/ml of IPN virus was multiphasic. When formalin-treated virus was titrated, cytopathic effect was delayed.

Under a UV intensity of 2000 $\mu W/cm^2$, the infectivity of 10^7 $TCID_{50}$/ml of virus was lost exponentially during the first 6 min of exposure after which it abruptly leveled off. The curve was less steep and curvilinear under an intensity of 440 $\mu W/cm^2$. The level of tailing was the same in both cases.

IPN virus was predictably stable at pH 7 at 4 C. A surprising 0.001% of an original concentration of 10^7 $TCID_{50}$/ml survived incubation at pH 9 and 2 for 5 wk. The reported survival of IPN virus in homeothermic animals was related to its ability to withstand prolonged exposure to low pH and to its relative heat stability.

MACKELVIE, R. M., AND DENISE DESAUTELS. 1975. Fish viruses — survival and inactivation of infectious pancreatic necrosis virus. J. Fish. Res. Board Can. 32: 1267–1273.

Nous avons étudié la survivance du virus de la pancréatite infectieuse nécrosante (PIN) dans des conditions propres à sa conservation en laboratoire, ainsi que son inactivation par plusieurs moyens physiques et chimiques.

Environ 99.9% de la virulence disparaît quand le virus de la PIN ($10^{6.5}$ – $10^{7.0}$ de la dose de culture tissulaire infectant 50% des individus, $DTCI_{50}$/ml) lavé, en suspension dans une saline tamponnée de phosphate (STP) et dans le milieu de culture essentiel minimal d'Eagle dilué à 1:10 avec STP, est maintenu à 4 C durant 1 année. Après 2 ans, plus de 10^2 de la $DTCI_{50}$/ml se trouve encore dans les deux suspensions. Le virus survit tout aussi bien dans le glycérol à 20 et 50%.

L'inactivation du virus de la PIN par la chaleur à 60 C se fait selon un processus à deux composantes, chaque composante se conformant à une cynétique de premier ordre. A un pH neutre, la virulence de 10^7 $DTCI_{50}$/ml est réduite de 99.9% durant les 30 premières mn d'exposition. Au bout de 5 h, 0.0001% sont encore vivants. Le taux d'inactivation de la première composante rapide augmente par ajustage du pH à 3 et à 10.

La courbe d'inactivation de $10^{6.5}$ $DTCI_{50}$/ml du virus de la PIN par la formaline à 1:4000 est polyphasée. Quand le virus traité à la formaline est titré, l'effet cytopathique est retardé.

A une intensité de rayons UV de 2000 $\mu W/cm^2$, la virulence de 10^7 $DTCI_{50}$/ml de virus disparaît à un taux exponentiel durant le 6 premières mn d'exposition, pour ensuite se stabiliser abruptement. La courbe est moins raide et curvilinéaire avec une intensité de 400 $\mu W/cm^2$. Le palier d'étalement est le même dans les deux cas.

Comme on devait s'y attendre, le virus de la PIN est stable au pH 7 à 4 C. Par ailleurs, un 0.001% inattendu d'une concentration initiale de 10^7 $DTCI_{50}$/ml survécut à une incubation de 5 semaines aux pH 9 et 2. Nous attribuons la survivance du virus de la PIN signalée chez les animaux homothermiques à son aptitude à supporter une exposition prolongée à un pH bas et à sa stabilité relative à la chaleur.

Received February 5, 1975
Accepted April 14, 1975

Reçu le 5 février 1975
Accepté le 14 avril 1975

Printed in Canada (J3720)
Imprimé au Canada (J3720)

THE importance of the virus disease, infectious pancreatic necrosis (IPN), to the culture of salmonid species in the Maritime provinces of Canada has recently been discussed (Desautels and MacKelvie 1975). The serious consequences of inadequate control over the spread of the virus were stressed in view of its ability to survive for extended periods in both fresh and salt waters and its resistance to two commonly used disinfecting agents. The parameters examined were those associated with the practical environment of fish rearing operations. The present report concerns the survival and inactivation of IPN virus in terms that are oriented toward its laboratory manipulation for diagnostic and research procedures, although it is recognized that some of the findings might be usefully extended to field application. Survival of the agent in several laboratory media was studied as well as its inactivation by heat, formalin, ultraviolet light, and the action of hydrogen ion.

Materials and Methods

CELL CULTURES, VIRUS, AND VIRUS ASSAY

The cell cultures, the virus, and its method of assay are the same as previously reported (Desautels and MacKelvie 1975) except that only the ATCC strain VR 299 of IPN virus was used in these studies. A further exception was the manner of harvest of the virus for certain experiments as indicated subsequently.

LABORATORY MEDIA FOR SURVIVAL STUDIES

The suspending media selected for these tests included Dulbecco's phosphate buffered saline (PBS), Eagle's Minimal Essential Medium (MEM) containing 10% fetal bovine serum (FBS) and antibiotics (100 IU penicillin, 100 μg streptomycin, and 25 μg nystatin/ml) diluted 1:10 in PBS, 20% glycerol in distilled water, and 50% glycerol in distilled water. Samples were stored at 4 C and portions removed bimonthly for titration for viral activity.

HEAT INACTIVATION

Washed IPN virus was suspended in Eagle's MEM (pH 6.8) and also in Eagle's MEM (containing 10% FBS) with pH adjusted variously to 9.0, 7.0, and 3.0. The virus suspensions were distributed in 1.0-ml amounts into Kahn tubes which were placed in a 60 C waterbath. At specified times thereafter samples were removed, rapidly cooled, and titrated for viral activity.

FORMALIN INACTIVATION

Formaldehyde solution from a freshly opened bottle (Fisher guaranteed analysis 37.1% HCHO) was diluted 1:4000 with indicator-free PBS containing washed IPN virus. The 50-ml reaction mixture (pH 7.2 and containing approximately 93 μg/ml formaldehyde) was incubated at 4 C. At zero time and specified intervals subsequently, 5.0-ml aliquots were withdrawn, and the formalin was neutralized by the addition of 0.1 ml of a 2% aqueous solution of sodium bisulfite and titrated for viral activity.

Controls run in connection with this procedure monitored the monolayer development of normal cells and cells to which neutralizer and neutralized formalin had been added. Virus-positive controls included the addition of virus to normal cells, incubation of neutralizer and neutralized formalin with virus for 30 min at 18 C before addition to cells, and incubation of cells with neutralizer and neutralized formalin for 30 min at 18 C before the addition of virus.

UV INACTIVATION

Clarified growth medium (containing phenol red) removed from IPN virus-infected cultures after attainment of maximal cytopathic effect (CPE) was placed to a depth of 3–4 mm in each of two petri dishes. The dishes were placed on magnetic stirrers below a General Electric germicidal UV lamp (G30T8) with a wave length of 254 nm. The intensity of the light striking the surface of the suspensions was measured using a model J225 Blak-Ray Ultraviolet Intensity Meter.[1] The virus suspensions were stirred continuously during the experiment. At appropriate times, samples were removed from both dishes and held at 0 C until titrated.

HYDROGEN ION INACTIVATION

Five-milliliter aliquots of growth medium fluid removed from cultures with advanced IPN virus-induced CPE were dialyzed at 4 C against 20 vol of buffers at pH 2.0 (0.1 M KCl–HCl), 7.1 (PBS) and 9.0 (0.1 M 2-amino-2-methyl-1, 3-propanediol). Equilibration of pH was attained within half an hour. The buffers were changed every second day. On every fifth day, a tube from each of the pH 2.0 and 9.0 buffers was removed and suspended in PBS at pH 7.1 for 4 h to restore neutrality. The concentrations of virus in these two tubes as well as a control tube (PBS dialysis) were measured.

Survival in Laboratory Suspending Media

Survival studies of IPN virus in which an initial concentration of $10^{6.5}$–$10^{7.0}$ $TCID_{50}$ of washed virus per milliliter was suspended in various media at 4 C were conducted for a period in excess of 1 yr (Fig. 1). All data were subjected to regression analysis and the coefficients of correlation were high ($r = -.84$ to $-.92$). The loss of infectivity of IPN virus suspended in MEM diluted with buffered saline and in PBS appeared to follow first-order kinetics for the 55-wk period and at least 10^3 $TCID_{50}$/ml remained in both media. Survival rate was slightly less in the saline diluted MEM than in PBS. Supplementary

---

[1] Ultra-violet Products, Inc., San Gabriel, Calif.

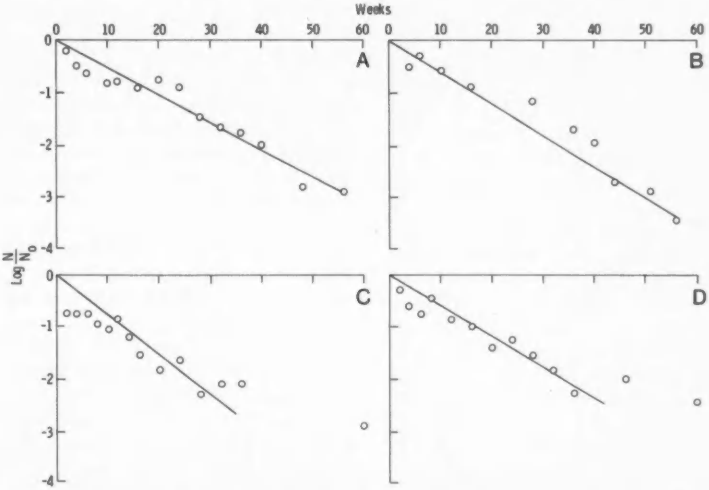


FIG. 1. Survival of washed IPN virus in laboratory reagents at 4 C. A, Phosphate buffered saline; B, Minimal Essential Medium with 10% FBS and antibiotics diluted 1:10 with phosphate buffered saline; C, 50% glycerol in distilled water; D, 20% glycerol in distilled water.

titrations performed after storage for 109 wk showed that the respective concentrations were $10^{2.3}$ and $10^{2.7}$ $TCID_{50}$/ml, and that the loss of activity had thus ceased to be first-order reaction. Refrigeration of virus harvests in the form of supernatant culture fluids (diluted 1:10 with PBS to stabilize pH) is a convenient way to store virus for routine inoculations and during the accumulation of bulk quantities. Our data indicate that this process is safely applicable to IPN virus. They also indicate the excellent stability of this virus when washed and suspended in PBS in which form it is often used in general experimentation, for the production of specific antiserum, and as control antigen in serum neutralizations tests.

The 1-yr survival patterns of IPN virus in 20 and 50% aqueous dilutions of glycerol closely paralleled each other, and those for the salt solutions. Glycerol stability was early recognized as a characteristic of IPN virus by Wolf et al. (1960) who reported its preservation in diseased tissue held in 50% glycerol at 4 C for 2.5 yr. The relatively innocuous effect upon IPN virus of storage in glycerol has been further commented upon (Wolf 1964, 1966); however, one strain (Kerlo) was reported to show no infectivity after 3 mo in 50% glycerol at 4 C (Wolf and Quimby 1971). Our more extensively quantitated data confirm the earlier reported glycerol stability of IPN virus, a characteristic that presently renders it unique among the known fish viruses.

Inactivation by Heat

At 60 C, IPN virus was inactivated in a two-component fashion, each component following first-order kinetics (Fig. 2A). An initial concentration of $10^{7.2}$ $TCID_{50}$/ml of IPN virus at neutral pH lost 99.9% of its infectivity in the 30-min duration of the first rapid component of inactivation. After 5 h one-millionth part of the original population had survived. The presence of 10% FBS in the suspending medium afforded only minimal protection.

This type of curve is similar to the 60 C thermal inactivation curves of foot-and-mouth disease virus (FMDV) (Bachrach et al. 1957) and vaccinia virus (Kaplan 1958) and the 50 C inactivation of several poliovirus strains (Youngner 1957). However, in contrast to our finding with IPN virus, these authors showed that under similar conditions of temperature and pH, a 99.9% loss of infectivity occurred after only 10 s for FMDV and 5 min for vaccina virus.

This order of heat stability has not previously been reported for IPN virus. The early literature states that inocula prepared from diseased fry held frozen for up to 4.5 yr or in 50% glycerol at 4 C for 2.5 yr were unable to produce cytopathic degeneration after being heated at 60 C for 1 h (Wolf et al. 1960). In these instances the concentrations of the virus in the inocula may have been sufficiently low that the limit of sensitivity of the assay system was reached relatively rapidly. A subsequent article reported the detection of infectivity in cell culture harvests after 60 min at 60 C, but this infectivity was destroyed if the pH

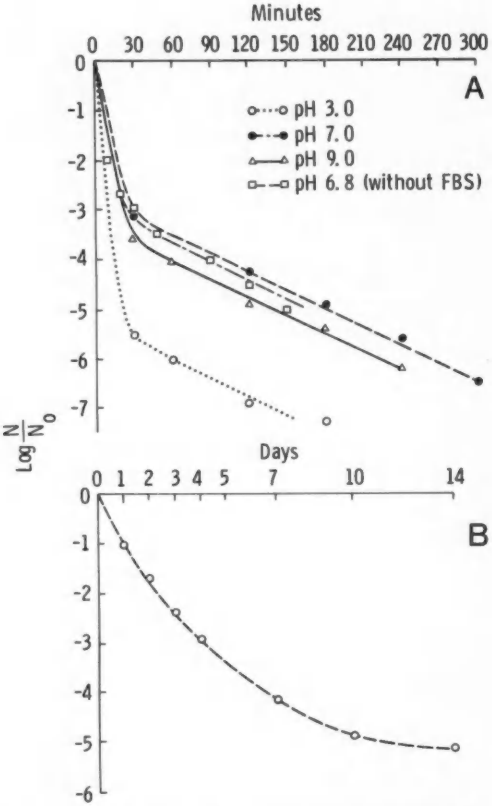


FIG. 2. A, Heat inactivation of washed IPN virus at 60 C in Minimal Essential Medium containing 10% fetal bovine serum except as indicated; B, Formalin inactivation of IPN virus at 4 C by a 1:4000 dilution of a commercial formaldehyde solution.

were adjusted to values of 3 or 10 (Wolf 1966). Our data confirm the ability of pH to affect the rate of thermal inactivation of IPN virus; however, this effect was limited to the initial, rapid phase of the biphasic heat inactivation process. The relative heat stability of IPN virus is consistent with reports of its survival in homeothermic hosts; for 24 h in the digestive tracts of chicken, owl, and mink (Sonstegard and McDermott 1972); in the excreta of gulls up to 8 days after gastric tube feeding of virus (Eskildsen and Jorgensen 1973) and for 21 days in the tissues of Swiss albino mice (Angiolelli and Rio 1971). Our results indicating the heat stability of IPN virus emphasize the danger inherent in the sometime practiced incorporation of "pasteurized" fish scrap in fish diets.

Inactivation by Formalin

At pH 7.2, the inactivation of $10^{6.5}$ $TCID_{50}$/ml of IPN virus at 4 C by a 1:4000 dilution of formalin was multiphasic and appeared to be asymptotic (Fig. 2B). Ten percent of the initial infectivity survived for 24 h, 0.1% for 4 days, and 0.001% for 14 days. A delay in the appearance of CPE in the titration monolayers of formalin-treated virus was observed. Control monolayers to which formalin neutralized with sodium bisulfite or sodium bisulfite alone had been added developed normally. All virus-positive controls showed rapid development of typical CPE.

Formalin inactivation of viruses has been reported to be monophasic (Charney et al. 1957; Bachrach et al. 1957), biphasic (Timm et al. 1956; Gerber et al. 1961; Darwish and Hammon 1966), and multiphasic (Gard 1955; Lycke 1958; McLean 1960). This variance in inactivation kinetics is related to the nature of the virus, differences in the conditions employed (particularly temperature), the timing of the sampling, the duration of the observation period and the assay procedure, especially in the region approaching the practical limits of detectability. The inctivation curve of IPN virus is a curving line similar to that found by Gard (1955) for the inactivation of poliovirus under nearly similar conditions. Such a curve does not lend itself to extrapolation whereby a prediction of safety may be made in the preparation of killed vaccine. Elevation of the temperature in the formaldehyde inactivation of poliovirus, besides yielding a steeper slope to the inactivation curve, also promoted linearity in the region of low virus concentration, thus facilitating prediction of zero infectivity (Salk and Gori 1960). Experiments to determine the existence of this phenomenon in the inactivation of IPN virus as well as the effect of higher temperature inactivation on maintenance of antigenic integrity and a critical matching of these findings would be prerequisite to the production of a vaccine against this disease. The delay in the appearance of CPE in the titration monolayers of formalin-treated IPN virus was similar to that noted for vacuolating virus (SV40) (Gerber et al. 1961), all three types of poliovirus, and certain other viruses (McLean 1960). It is important to be aware of the existence of this phenomenon when attempting to determine a safe endpoint for the inactivation process.

Inactivation by UV Light

Data obtained from experiments in which $10^{7.0}$ $TCID_{50}$/ml IPN virus were irradiated with two intensities of UV light ($\lambda = 254$ nm) are shown in Fig. 3A. At 2000 μW/cm^2, infectivity was lost exponentially during the first 6 min of exposure after which the curve abruptly leveled off. At 440 μW/cm^2, the inactivation curve was less steep and curvilinear; however, it leveled off after the same degree of inactivation had been achieved as with the higher intensity irradiation. Because the tailing effect of both these curves showed minimal declination, we conclude that one tissue culture dose per million is enduringly resistant to the action of UV irradiation. Although it is possible that a higher UV intensity for a shorter period might inactivate more virus, further treatment would probably be more damaging to viral antigenicity, retention of which is vital to vaccine production, than to infectivity which is associated with the nucleic acid. For this reason and also because of the general phenomenon of repair mechanisms able to reactivate UV-injured viruses, irradiation in combination with other inactivating agents may be more effective for this purpose. The application of UV energy, insufficient for intensive killing, is reported to exert a sensitizing effect upon viruses such that UV-treated suspensions exposed to further unfavorable conditions such as heat (Shaughnessy et al. 1957) or chemicals (Taylor et al. 1957) can be inactivated to safe levels more readily. The relative merits of attenuated vs. killed vaccine are still being debated. An attenuated, live vaccine of IPN virus has shown promise in coho fry (McMichael 1974). Use of a killed IPN vaccine has still to be attempted.

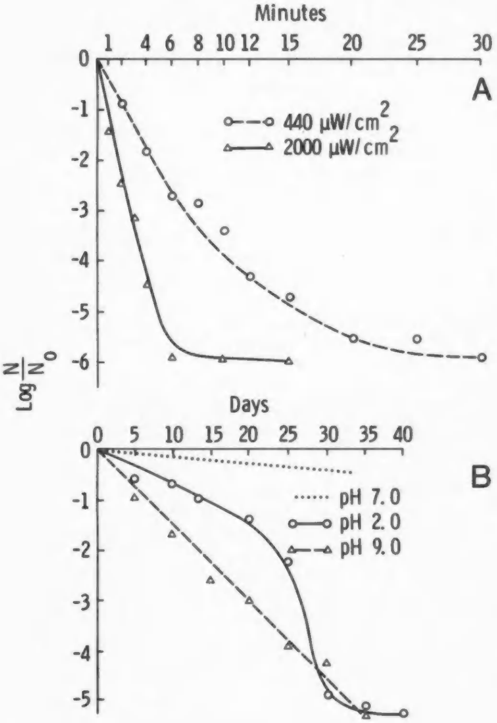


FIG. 3. A, UV inactivation ($\lambda = 254$ nm) at two light intensities of a stirred suspension of IPN virus in clarified growth medium at room temperature; B, Hydrogen ion inactivation of IPN virus by dialysis at 4 C against buffers at various pH.

Our data cannot be usefully related to disinfection procedures designed to rid influent hatchery waters of IPN virus because of the great number of variables associated with such systems. However, it might be expected that the residual resistant fraction found under our experimental conditions would also appear under field conditions and should be taken into consideration. In the laboratory the danger of relying solely on UV light to disinfect spilled IPN virus in sterile work areas is evident.

Inactivation by Hydrogen Ion

IPN virus ($10^{7.0}$ TCID$_{50}$/ml) at 4 C was predictably stable at pH 7.0, but was unexpectedly resistant to inactivation by nonphysiological pH (Fig. 3B). A 0.001% survival was demonstrated after 5 wk of exposure to pH 9.0 and 2.0. At pH 9.0, the reaction appeared to follow simple first-order kinetics; these results parallel those obtained in the pH study of FMDV (Bachrach et al. 1957). At pH 2.0 the inactivation curve was composed of possibly three components with a line of steeper slope beginning at 3 wk and leveling off at 5 wk. However, in distinct contrast to IPN virus which demonstrated residual activity after many weeks, the rates of inactivation of FMDV at pH values of 2, 3, and 4 were too rapid to be measured. Treatment at pH 2.0 is a common procedure to inactivate viruses used in the experimental production of interferon. Dialysis against a pH 2.0 buffer for 2 or 3 days at 4 C is generally considered to be sufficient to destroy viral inducers, but a more resistant virus such as Newcastle disease virus should be treated for 4 days for total destruction (Lockhart 1973). The unusual stability at pH 2.0 that we have demonstrated for IPN virus is in contrast to the acid-sensitivity found by Ditchfield as reported by Wolf (1966). However, it is corroborated to some extent by Vestergaard-Jorgensen (1973) who found virtually no loss when IPN virus strain Sp was held at pH 2.5 for 60 min. It is known that strains of viruses may differ in pH stability pattern. This was shown for IPN virus by Wolf and Quimby (1971) who found the French strain to be more stable at pH 5.9 than at pH 7.0 at which value the reference strain VR299, used in this study, is most stable.

There is evidence that acid resistance is a characteristic of enteroviruses as a group and one can speculate that this resistance would protect enteric viruses from inactivation by gastric juice during passage through the stomach (Plotkin et al. 1962). IPN virus fed to herons, mergansers, owls, and mink was recovered from the feces of some of these birds and the mink. The virus, therefore, survived the acidity of the stomach of these animals and one would surmise it would do likewise in fish where the pH of the stomach of brook trout 4 h after feeding was found to be 3.2. Experimental infection has indeed been accomplished by the oral route (Snieszko and Wolf 1958; McMichael 1974) and doubtless the demonstrated acid-resistance was an important contributing factor.

Conclusions

IPN virus stored in PBS, MEM, and in 50 and 20% glycerol is stable for prolonged periods of time at 4 C, indicating that these laboratory reagents provide a good means of maintaining the virus for laboratory manipulations.

The resistance of IPN virus to both physiological and nonphysiological pH as well as to heat provides further substance to the suggestion of the oral–fecal route in the epidemiology of IPN.

The curve of IPN virus survival under UV irradiation and formalin treatment proceeds asymptotically toward zero; this tailing indicates a need for caution in production of an IPN vaccine.

Acknowledgments

We thank Dr W. D. Paterson for his review of this manuscript and for his helpful comments.

Angiolelli, R., and G. J. Rio. 1971. The Swiss/ICR (Ha) albino mouse as an experimental host for infectious pancreatic necrosis virus of trout. J. Fish Biol. 3: 139–144.

Bachrach, H. L., S. S. Breese Jr., J. J. Callis, W. R. Hess, and R. E. Patty. 1957. Inactivation of foot-and-mouth disease virus by pH and temperature changes and by formaldehyde. Proc. Soc. Exp. Biol. Med. 95: 147–152.

Charney, J., W. P. Fisher, and R. A. MacLlowitz. 1957. Preparation and inactivation of purified poliovirus: comparison of vaccines derived from Mahoney and Parker poliovirus. Proc. Soc. Exp. Biol. Med. 96: 601–605.

Darwish, M. A., and W. M. Hammon. 1966. Japanese B. encephalitis virus vaccines from tissue culture. VII. Formalin inactivated Nakayama strain vaccine. Proc. Soc. Exp. Biol. Med. 122: 813–816.

Desautels, D., and R. M. MacKelvie. 1975. Practical aspects of survival and destruction of infectious pancreatic necrosis virus. J. Fish. Res. Board Can. 32: 523–531.

Eskildsen, U. K., and P. E. V. Jorgensen. 1973. On the possible transfer of trout pathogenic viruses by gulls. Riv. It. Piscic. Ittiop. VIII: 104–105.

Gard, S. 1955. Discussion panel, p. 202. *In* Poliomyelitis, papers and discussions presented at 3rd Int. Poliomyelitis Conf., J. B. Lippincott Company, Philadelphia, Pa.

Gerber, P., G. A. Hottle, and R. E. Grubbs. 1961. Inactivation of vacuolating virus (SV40) by formaldeyhde. Proc. Soc. Exp. Biol. Med. 108: 205–209.

Kaplan, C. 1958. The heat inactivation of vaccinia virus. J. Gen. Microbiol. 18: 58–63.

Lockart, R. Z. 1973. Criteria for acceptance of a viral inhibitor as an interferon and a general description of the biological properties of known interferons, p. 11–27. *In* N. B. Finter [ed.] Interferons and interferon inducers. American-Elsevier Publishing Co., Inc., New York, N.Y.

Lycke, E. 1958. Studies of the inactivation of poliomyelitis virus by means of treatment with formaldehyde. Ph.D. Thesis. Karolinska Institutet, Stockholm.

McLean, I. W. Jr. 1960. Panel discussion. Ann. N.Y. Acad. Sci. 83: 753–760.

McMichael, J. S. 1974. The isolation, comparison and attenuation of several viruses infecting Oregon salmonids. Ph.D. Thesis. Oregon State Univ., Corvallis, Oreg.

Plotkin, S. A., R. I. Carp, and A. F. Graham. 1962. The polioviruses of man. Ann. N.Y. Acad. Sci. 101: 357–389.

Salk, J. E., and J. B. Gori. 1960. A review of theoretical, experimental and practical considerations in the use of formaldehyde for the inactivation of poliovirus. Ann. N.Y. Acad. Sci. 83: 609–637.

Shaughnessy, H. J., A. M. Wolf, M. Janota, J. Neal, F. Oppenheimer, A. Milzer, H. Naftulin, and R. A. Morrisey. 1957. Immunogenicity of poliomyelitis vaccine prepared with ultraviolet irradiation and mild heat. Proc. Soc. Exp. Biol. Med. 95: 251–255.

Snieszko, S. F., and K. Wolf. 1958. Infectious pancreatic necrosis of salmonid fishes (acute catarrhal enteritis). U.S. Dep. Inter. Fish. Leafl. 453.

Sonstegard, R. A., and L. A. McDermott. 1972. Epidemiological model for passive transfer of IPNV by homeotherms. Nature 237: 104–105.

Taylor, A. R., W. W. Kay, E. A. Timm, A. E. Hook, and I. W. McLean Jr. 1957. Inactivation of poliomyelitis virus for the preparation of vaccines. J. Immunol. 79: 265–275.

Timm, E. A., I. W. McLean Jr., C. H. Kupsky, and A. E. Hook. 1956. The nature of the formalin inactivation of poliomyelitis virus. J. Immunol. 77: 444–452.

VESTERGAARD-JORGENSEN, P. E. 1973. Inactivation of IPN and Egtved virus. Riv. It. Piscic. Ittiop. VIII: 107–108.

WOLF, K. 1964. Characteristics of viruses found in fishes. Dev. Ind. Microbiol. 5: 140–148.

1966. The fish viruses, p. 35–101. *In* K. M. Smith and M. A. Lauffer [ed.] Advances in virus research. Vol. 12. Academic Press, Inc., London and New York.

WOLF, K., C. DUNBAR, AND S. F. SNIESZKO. 1960. Infectious pancreatic necrosis in trout. I. A tissue culture study. Prog. Fish Cult. 22: 64–68.

WOLF, K., AND M. C. QUIMBY. 1971. Salmonid viruses: infectious pancreatic necrosis virus. Arch. Gesamte Virusforsch. 34: 144–156.

YOUNGNER, J. S. 1957. Thermal inactivation studies with different strains of poliovirus. J. Immunol. 78: 282–290.

Limited Arsenic Dispersion in Sea Water, Sediments, and Biota Near a Continuous Source

WILLIAM R. PENROSE, ROBERT BLACK, AND MICHAEL J. HAYWARD

Department of the Environment, Fisheries and Marine Service, Biological Station, St. John's, Nfld.

PENROSE, W. R., R. BLACK, M. J. HAYWARD. 1975. Limited arsenic dispersion in sea water, sediments, and biota near a continuous source. J. Fish. Res. Board Can. 32: 1275–1281.

Moreton's Harbour, Newfoundland, has been exposed to arsenic-bearing drainage and leaching from a stibnite mine for at least 38 yr and possibly longer than 84 yr. Measurements of inorganic arsenic in sea water and sediments and total arsenic in some marine organisms revealed a very limited influence of continuous exposure to arsenic in the small harbor. Arsenic concentrations in surface water declined to normal within 200 m, and in sediments within 50 m. Animals did not show significantly higher levels nearer the mine, with the exception of the sea urchin *Strongylocentrotus droebachiensis*, which accumulated significantly higher levels of arsenic adjacent to the mine site.

PENROSE, W. R., R. BLACK, AND M. J. HAYWARD. 1975. Limited arsenic dispersion in sea water, sediments, and biota near a continuous source. J. Fish. Res. Board Can. 32: 1275–1281.

Le hâvre de Moreton Terre-Neuve, a été exposé durant au moins 38 ans, possiblement durant plus de 84 ans, aux eaux de drainage et de lessivage contenant de l'arsénic d'une mine de stibnite. Des mesures d'arsénic inorganique dans l'eau de mer et dans les sédiments et d'arsénic total dans certains organismes marins indiquent que l'exposition continue à l'arsénic dans le petit port a eu une influence très limitée. Les concentrations d'arsénic dans l'eau de surface diminuent et atteignent un niveau normal en dedans de 200 m, et dans les sédiments, en dedans de 50 m. Les animaux ne montrent pas de niveaux significativement plus élevés près de la mine, sauf l'oursin de mer, *Strongylocentrotus droebachiensis*, qui accumule des niveaux d'arsénic significativement plus élevés dans le voisinage de la mine.

Received May 3, 1974
Accepted April 2, 1975

Reçu le 3 mai 1974
Accepté le 2 avril 1975

As part of a broader study of the sources, dispersion, and metabolism of arsenic in the marine environment, an abandoned stibnite mine at Moreton's Harbour, Newfoundland, provided an opportunity to study the behavior of arsenic emitted from a point source.

Moreton's Harbour is located on New World Island, on the northeast shore of Newfoundland, in an area noted for its variety of mineral deposits. The local formation, known as Moreton's Volcanics, is extrusive igneous and sedimentary rocks of the Ordovician (Heyl 1936) and contains numerous deposits rich in arsenic. Three shafts have been worked around Moreton's Harbour. One of these is cut into a cliff next to the sea (Fig. 1, station 1), and was mined sporadically for stibnite from before 1890 until 1916. We have found that the water draining from the mine during periods of runoff contained high levels of arsenic. The gravel of the intertidal beach in front of the mine contained large quantities of arsenic.

We suspected that the rate of entry of arsenic into the sea from this source might be large enough to affect the content of this element in sessile and sedentary organisms. We examined the changes in arsenic concentrations in sea water, sediments, and organisms with increasing distance from the source.

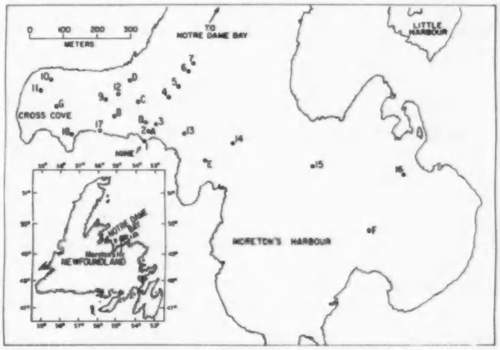


FIG. 1. Sampling stations in Moreton's Harbour, Notre Dame Bay, Nfld.

Printed in Canada (J3410)
Imprimé au Canada (J3410)

Methods

SAMPLING

Surface water samples were taken in acid-washed polyethylene bottles; there was no loss of arsenic from samples on storage for a few days and seawater samples were stable indefinitely. Sediment samples and sand dollars were collected with a Petersen dredge (stations 1–16). Sediment samples, sea urchins, and some other fauna were also collected by diver (stations A–G) using plastic corer-liner tube and stoppers to take short sediment columns. The water trapped above each sediment column was used as a bottom water sample. Core samples and fauna were frozen in dry ice for transport. Some samples of algae and fauna were collected from the shore or with small baited traps.

Stations were located using a magnetic sighting compass and a chart prepared from air photos. Data collected by Environment Canada meteorological stations in Baie Verte, Grand Falls, and Bonavista were used to estimate the rainfall in the New World Island area.

SAMPLE PREPARATION AND ANALYSIS

The arsenic was concentrated from seawater samples by ferric hydroxide coprecipitation using a method similar to that of Thiel and Carpenter (1970). To 500 ml sea water was added 2 ml of a solution of 0.45 M ferric ammonium sulfate dissolved in 0.6 N HCl. Then 2.5 ml concentrated ammonia was added with stirring. After settling, most of the clear supernatant was drawn off and the precipitate filtered by gravity through Whatman #1 paper. The precipitate was dissolved with 40 ml 6 N HCl and diluted to 90 ml. A 45-ml aliquot or less was used in the arsenic determination.

Where cores were taken, the sediment-containing part of the tube was sawed off and the core extruded. It was cut as carefully as possible into 1-cm segments as it thawed. All sediment samples were dried at 80 C and the pebbles removed. The dried sediments were then ground to a fine powder and digested with nitric and sulfuric acids. The ice in the remainder of the coring tube was later thawed, filtered through Whatman #1 paper, and 100-ml samples were assayed for arsenic by coprecipitation.

Where nitric–sulfuric acid digestion was employed, the following procedure was followed: To a 1-g sample was added 5 ml of a cooled mixture of nitric and sulfuric acids (2:3, vol/vol). The flask was heated carefully while NO_2 fumes were evolved, then strongly until white SO_3 fumes appeared. The digest was cooled, 2 ml nitric acid was added, and the mixture again heated to white fumes. The cooled digest was diluted to 100 ml and the arsenic concentrated by coprecipitation as above.

The arsenic in tissue samples cannot be released quantitatively by acid digestion. Evans and Bandemer (1954) developed a method of dry ashing under oxidizing conditions. We used the method as modified by Spencer, Clarke, and Luscombe of the Fish Inspection Branch, Environment Canada, St. John's, Nfld. (unpublished; described here with permission):

Into 500 ml rapidly stirring water was mixed 30 g magnesium nitrate and 50 g light magnesium oxide. The resulting slurry was shaken before use.

A sample of not more than 2 g wet tissue or 0.5 g dried ground tissue was accurately weighed into a tared Virtis homogenizing vessel. Ashing slurry was added until the weight of sample plus slurry was 15.0 g. The sample was thoroughly homogenized until no distinct lumps of sample were visible. A 10.0-g portion was weighed into a 50-ml beaker.

Standards were prepared using sodium arsenite or arsenate standard solutions stirred into 10 g slurry. Samples from a single batch of dried, ground whole shrimp were frequently included to monitor the fidelity of the ashing and analytical procedures.

All samples were dried at 80 C. They were placed in a muffle furnace in a well-ventilated area (NO_2 is evolved) and heated for 1 h at 200 C, 1 h at 300 C, and 8 h at 500 C.

After cooling, the residue was dissolved in 20 ml 6 N HCl and transferred to a 125-ml filter flask; the beaker was rinsed with 25 ml water into the flask. To the contents of the flask were added in order: 0.2 ml of 0.45 M ferric ammonium sulfate in 0.6 N HCl; 2 ml of 15% aqueous KI; and 0.4 ml 40% $SnCl_2$ in concentrated HCl. To the sidearm of the flask was attached a rubber tube and a bent Pasteur pipet. In the pipet was a loose plug of cotton wool moistened with 10% lead nitrate. The tip of the pipet dipped into 3.0 ml of a solution of 0.5% silver diethylidithiocarbamate in pyridine.

The reaction was begun by adding 3 g 20-mesh granular zinc ("arsenic-free") to the flask, which was quickly stoppered. Where a sample had been coprecipitated and much iron was present, KI and $SnCl_2$ only were added; 6 g zinc shot (about 2 mesh) was used in place of granular zinc to moderate the reaction. Traces of generated arsine were swept into the colorimetric reagent with the large volumes of hydrogen evolved. After 30 min, the absorbance at 540 nm was measured. From time to time, or if the presence of antimony was suspected, absorbance was also measured at 500 nm; with the use of appropriate standards, the interference due to antimony could be calculated and subtracted. In the experiments reported in this paper, this interference was never observed.

Results

ANALYTICAL METHOD

The ferric hydroxide coprecipitation was found to quantitatively recover standard additions of 1 and 10 μg of arsenic (as sodium arsenate) from 500 ml sea water or fresh water, within the accuracy of the arsenic determination (0.2 μg). Since sediment samples were digested in groups, many samples were repeated from group to group to serve as internal monitors; the range only infrequently exceeded 10%.

TABLE 1. Comparison of sample decomposition methods.

Samples Chemical form	Amount of As added	Amount recovered (μg As) $HNO_3:H_2SO_4$	Dry ashing
Sodium arsenite	10 μg	10.8	9.8
Cacodylic acid	10	0.4	7.0–7.7
Arsanilic acid	10	10.5	10.3
Shrimp, dry, 1 g	—	<0.2	12.5[a]
Mussel, fresh, 1 g	—	<0.2	12.2[a]
Witch flounder muscle, fresh 1, g	—	<0.2	13.6

[a] Agrees with values measured by K. Spencer, Fish Inspection Branch, on same samples.

The method of dry ashing with magnesium nitrate gave acceptable reproducibility of arsenic concentrations in tissue samples. Five replicates run with a sample of dried, ground shrimp yielded a value of 12.4 ± 0.2 ppm. Eight replicates of cacodylic acid (18.4 μg each, equivalent to 10.0 μg As) gave 7.1 ± 0.6 μg As; this low yield may be attributable to the escape of arsenic as volatile products during ashing.

Table 1 contrasts the effectiveness of dry ashing and wet digestion with nitric and sulfuric acids. The aryl arsenic compound is easily decomposed by nitric acid, while the alkylated compound is extremely stable or decomposes to volatile products during the digestion. The arsenic in tissue samples is not detectable by wet digestion, but can be consistently measured by dry ashing. Because of the precision of arsenic recovery by dry ashing, results reported here are based on an assumption of 100% yield.

SOURCES OF ARSENIC

Arsenic was expected to enter the sea by means of runoff from the mine and solution from arsenic-rich gravel in the intertidal zone and sediments near the mine.

The mine consists of an upper trench and a lower shaft; the floor of the trench has collapsed partially into the shaft. Heyl (1936) reported a partial collapse, so this situation has existed for at least 37 yr. Drainage from the surrounding hillside percolates through the trench into the shaft and flows in a stream from the mouth of the shaft across 10 m of beach to the sea. After inspection of the area and study of a detailed chart, we estimated that the trench receives the runoff of about 1000 m^2. An inch (2.5 cm) of rainfall would result in 24,000 liters of water washing through the mine.

Two separate measurements of arsenic levels in the drainage water were made. The first, November 5, 1972, yielded a value of 595 parts per billion (ppb); during the previous 3 days, about 2 cm of precipitation had fallen as snow. The second, on December 20, 1972, was 182 ppb; no precipitation had fallen during the previous 3 days, but much snow remained on the ground. On both occasions the flow from the mine was considerable, about 20–50 liters/min. Based on these figures, a reasonable minimum estimate of outflow from the mine is about 10 g per 2.5 cm of rain. Since the annual rainfall in this area is about 40 inches (102 cm) the amount of arsenic washed into the sea over the past 40 yr would be at least 16 kg; if the rate of leaching has decreased with time, the actual amount of arsenic washed into the harbor may be greater.

The rate of solution of arsenic from sediments and arsenic-rich beach gravel is even more difficult to estimate. A sample of gravel from the beach contained 2600 ppm As and the sediment 34 m offshore (station 2) contained 847 ppm (Table 2). We would expect the rate of dissolution to depend on water temperature, mixing, and possibly biological action as well as more constant factors such as surface area, pH, oxygen and iron concentration (Seydel 1972).

In a simple experiment, sea water was allowed to stand over gravel taken from the beach near the low tide line. Even though the gravel had been exposed to sea water for an indefinite period on the beach, arsenic still leached from the gravel (Table 3).

ARSENIC IN SEA WATER

The inorganic arsenic content was measured in surface seawater samples taken on July 31, 1973, during a period of no precipitation (Table 2). There had been no drainage from the mine for many days. These values should then represent the arsenic originating from beach gravel and sediments alone. Because of the very small area

TABLE 2. Arsenic in sea water, sediments, and sand dollars in Moreton's Harbour.

Station	Radial distance from mine (*m*)	Inorganic As in sea water (*ppb*)	Inorganic As in sediments (*ppm*)[a]	Total As in sand dollars (*ppm*)[a]
1[b]	0	5.3	2600	—
2	34	4.1	847	—
3	65	—	11.0	1.8, 10.8
4	147	2.4	18.4	2.8
5	186	0.2	9.1	3.4, 4.0, 3.7, 1.6, 1.5
6	239	—	14.7	3.1
7	267	<0.2	13.3	—
8	113	2.6	16.2	—
9	163	<0.2	20.7	—
10	321	0.3	18.4	—
11	332	—	20.7	—
12	152	—	18.7	5.0, 3.9, 3.5, 2.9
13	118	1.4	27.6, 30.3	6.0, 4.5, 5.7
14	262	—	23.2	—
15	500	0.2	34.4	—
16	745	2.1	17.0	—

[a] Dry weight.

[b] Station 1 is the intertidal area at the beach in front of the mine.

TABLE 3. Dissolution of arsenic from gravel. Gravel collected from station 1 (250 g) was placed in 500-ml flasks and covered with 300 ml Millipore-sterilized sea water. The flasks were stored at room temperature. The sea water used contained 1.7 ppb arsenic at the beginning of the experiment.

	Arsenic in sea water (*ppb*)				
	20 days		43 days		145 days
Mean As (ppb)	166.3		242.0		247.5
SD	59.8		57.5		56.3
Sample size	16		15		16
Paired *t*		9.948 $P \ll 0.001$		0.233 $0.9 > P > 0.5$	

of arsenic-rich sediment, it was not surprising that the arsenic was quickly diluted to background levels. Similar results were obtained in the sea-water samples trapped in the coring tubes in the survey of September 1974 (Table 4). At this time also there was no drainage from the mine. These were samples of water in immediate contact with the sediments, yet the arsenic content over the heavily contaminated sediment was only slightly elevated. Arsenic levels at control stations at Whale's Gulch (5 km distant) and Middle Cove (300 km distant) both showed a background level of 0.9 ± 0.3 ppb.

In September 1972, the arsenic level at station 1 was 3.8 ± 0.6 ppb, although there was a considerable outflow from the mine with a measured arsenic level of 595 ppb. This was no higher than the values obtained during periods of no drainage. The mine drainage would therefore not appear to be an important source of the arsenic in the sea water; most of the arsenic must be derived by direct solution from the gravel and sediments in the intertidal and subtidal zones.

ARSENIC IN SEDIMENTS

In spite of the long history of the mine, the distribution of arsenic in the sediments has been very limited (Tables 2 and 4 and Fig. 1). Beyond the high level at stations 1, 2, and A, concentrations declined to a level which was more or less even throughout the harbor. The arsenic concentrations in surface sea water and sediments were significantly correlated ($r = .79, P < .01$).

Core samples were taken to ascertain that the rapid decline of sedimentary arsenic with distance was not an artifact of the mixing action of the Petersen dredge. Analysis of the top centi-

TABLE 4. Arsenic in bottom sea water, sediments, and sea urchins in Moreton's Harbour, September 1974. Sample size of sea urchins is in parentheses.

Station	Radial distance from mine (*m*)	Inorganic As in sea water above cores (*ppb*)	Inorganic As in top cm of sediment cores (*ppm*)	As in sea urchin gonads (ppm ± SD)
1[a]	0	4.4	—	6.0 ± 2.3 (3)
A	35	1.3, 1.9	562,508	5.6 ± 1.5 (4)
B	57	1.0	25.4	3.8 ± 0.9 (3)
C	117	.5	19.4	1.4, 1.3 (2)
D	180	.6	26.9	2.1 ± 1.0 (3)
E	189	<.5	27.1	1.9 ± 0.1 (3)
F	714	<.5	41.0	—
G	280	1.0, 0.3	16.0, 20.6	3.3 ± 0.5 (5)

[a] Same as station 1 in Fig. 1.

TABLE 5. Arsenic concentrations in sediments at various depths.

	As concn (*ppm*)				
	Sediment interval (*cm*)				
Station	0–1	1–2	2–3	3–4	4–5
A[a]	560, 510	630, 670	930, 1000	670, 870	690
B	25	30	27		
C	19				
D	27	—[b]	21		
E	27	—[b]	34		
F	41	64	51	52	51
G[a]	16, 21	14, 17	11, 9		

[a] Duplicate cores taken.
[b] Sample lost.

meter of the cores confirmed that the arsenic distribution pattern was essentially the same as indicated in the Petersen dredge survey (Table 4). At station A (Table 5) the highest arsenic levels were found in the 2–3 cm interval of both cores. This may represent deposition during the period of mining; if so, it indicates an unusually rapid sedimentation rate in the harbor, about 1 cm per 25 yr.

ARSENIC IN ORGANISMS

Sand dollars (*Echinarachnius parma*) were the only organisms recovered consistently in the Petersen dredge samples. The arsenic concentrations in the dried, ground animals (including test) did not decrease with distance from the mine (Table 2). (There was an isolated high measurement at station 3.)

Initial measurements made on sea urchins (*Strongylocentrotus droebachiensis*) indicated much higher levels in animals nearer the mine (80 ppm at station 1 vs. 5.4 ppm at station 10). These measurements were made on the entire body contents of individual animals, and by the time the animals of Table 4 were collected, it was recognized that these measurements were biased by the presence of sediment particles. When guts and gonads were dissected from organisms, it was observed that the guts showed a large difference in arsenic content with respect to distance from the mine (32 ppm at station A and 8 ppm at station G). Recognizable traces of sand remained when the dry-ashed gut samples were dissolved in acid. When gonads were examined, the difference was much less (station A: 4.2 ppm; station G: 3.4 ppm). Hence the results presented in Table 4 are limited to gonad tissue only. If the urchins over the high-arsenic (>500 ppm) sediment and over the low-arsenic (<50 ppm) sediment are grouped, the difference in arsenic concentration is still significant ($t = 5.33$, $P < .001$) though much smaller (5.8 ppm ± 1.7 SD vs. 2.5 ± 1.1).

Miscellaneous organisms were collected at vari-

TABLE 6. Arsenic concentrations in organisms found in Moreton's Harbour.

Organism and location	As concn (*ppm* ± SD)	*t*-test
Mytilus edulis (except shell)		
Station 1	5.3±5.4 (n = 8)	$t = 1.89$, n.s.[a]
Station 10	1.6±0.9 (n = 13)	
Control sites[b]	1.6±0.5 (n = 4)	
Littorina littorea (except shell)		
Station 1	11.5, 15.0 (n = 2)	n.a.[a]
Control sites	4.0±2.5 (n = 5)	
Fucus sp.		
Station 1	17.2±7.8 (n = 10)	$t = 1.00$, n.s.
Control sites	12.1±6.6 (n = 3)	
Ascophyllum nodosum		
Station 1	17.2±2.5 (n = 3)	$t = 3.9, P < .01$
Control sites	9.8±2.0 (n = 3)	
Cunner (*Tautogolabrus adspersus*), muscle		
Station 7	0.6±0.9 (n = 6)	
Blenny (sp. unknown), muscle		
Station 1	0.8 (n = 1)	n.a.
Station 7	0.4 (n = 1)	
Lobster (*Homarus americanus*), muscle		
Station 1	3.8 (n = 1)	n.a.
Station A	7.6 (n = 1)	

[a] n.s. = not significant; n.a. = *t*-test not applicable.

[b] Control sites are either Whale's Gulch (5 km distant) or Middle Cove (300 km distant).

ous stations. In no case does there appear to be a notable accumulation of arsenic (Table 6). The levels observed in lobster are not at all high. We have observed 4.4 ppm in commercial lobster; Chapman (1926) found 31–110 ppm and Lunde (1970) 5.8 ppm in lobster muscle.

Discussion

The effect of long-term concentrated source of arsenic in this confined harbor is surprisingly limited. Instead of the expected gradient of arsenic in the sediments as a function of distance from the mine, an abrupt decrease was observed between stations 2 and 3 (31 m apart) and A and B (22 m apart). Stations 2 and A are near enough to shore that the arsenic present could have been deposited there by wave action or mining operations.

It is interesting to note that the concentrations of arsenic both in the mine drainage and in the laboratory solubilization experiments are within a relatively narrow range (100–600 ppb). Since the concentrations in the laboratory experiments increased little between 43 and 145 days' exposure, these may approximate equilibrium concentration of arsenic in water in contact with this particular source mineral. The relatively low concentration measured in sea water immediately in front of the mine (station 1) indicates that little of this arsenic is likely to be absorbed by the sediments; arsenic entering the sea from the mine or through dissolution of sediments may remain in solution, to be diluted and dispersed by tides and currents.

Among the organisms sampled, the sea urchins displayed significantly higher arsenic concentrations nearer the mine. One species of macroalgae (a major component of the urchin's diet) also seems to accumulate higher arsenic levels nearer the mine (Table 6) although the sample size is very small. In laboratory experiments the arsenic in algae consumed by urchins was released into the sea water in a soluble, organic form (Black, unpublished data) and there was no gain or loss of arsenic by the animals during a 50-day period. Arsenic-containing sediment particles in the urchins' intestines present a concentrated source of inorganic arsenic that may be the main source of the element. It is unlikely that arsenic is absorbed from sea water due to the very low concentrations involved.

Arsenic may be highly overrated as a potential pollutant (Frost 1967, 1970). Marine animals, at least, seem to possess the potential to deal with this element, which is moderately toxic in the inorganic state, by converting it to an organic derivative that is biologically and chemically stable (Chapman 1926; Sachs et al. 1971; Lunde 1969; Penrose unpublished data), and probably nontoxic

(Coulson et al. 1935; Frost 1967, 1970). The work of Seydel (1972) and Isensee et al. (1973) as well as our own data (Table 6) indicates that concentrations are not magnified in food chains, at least as a general phenomenon. It is likely that the physical transport of the element in the dissolved state is unrelated to its transport in the solid state, so that particulate arsenic-containing material would be expected to remain within a relatively restricted area around an outfall, while dissolved arsenic should remain in solution until thoroughly dispersed. In this respect, it is quite unlike mercury, for example, whose water–sediment interactions are highly complex (Gavis and Ferguson 1972).

Acknowledgments

Mr G. Tucker collected the core and fauna samples. The technical assistance of Mr W. Squires in some of the analyses and in calculating annual rainfall is appreciated. An accurate chart of the Moreton's Harbour area was provided by Drs R. V. Gibbons and V. S. Papezik of the Geology Department of Memorial University of Newfoundland. Mr K. Spencer of the Inspection Branch of the Fisheries and Marine Service, St. John's, saved us much time by providing an unpublished analytical procedure for total arsenic.

CHAPMAN, A. C. 1926. The presence of compounds of arsenic in marine crustaceans and shell fish. Analyst 51: 548–563.

COULSON, E. J., R. E. REMINGTON, AND K. M. LYNCH. 1935. Metabolism in the rat of the naturally occurring arsenic of shrimp as compared with arsenic trioxide. J. Nutr. 10: 255–270.

EVANS, R. J., AND S. L. BANDEMER. 1954. Determination of arsenic in biological materials. Anal. Chem. 26: 595–598.

FROST, D. V. 1967. Arsenicals in biology — retrospect and prospect. Fed. Proc. Fed. Am. Soc. Exp. Biol. 26: 194–208.

1970. Tolerances for arsenic and selenium: a psychodynamic problem. World Rev. Pest Control 9: 6–27.

GAVIS, J., AND J. F. FERGUSON. 1972. The cycling of mercury through the environment. Water Res. 6: 989–1008.

HEYL, G. R. 1936. Geology and mineral deposits of the Bay of Exploits area. Newfoundland Dep. Nat. Resour. Bull. 3: 39–50.

ISENSEE, A. R., P. C. KEARNEY, E. A. WOOLSON, G. E. JONES, AND V. P. WILLIAMS. 1973. Distribution of alkyl arsenicals in a model ecosystem. Environ. Sci. Technol. 7: 841–845.

LUNDE, G. 1969. Water soluble arseno-organic compounds in marine fishes. Nature 224: 186–187.

1970. Analysis of arsenic and selenium in marine raw materials. J. Sci. Food Agric. 21: 242–247.

SACHS, R. M., J. L. MICHAEL, F. B. ANASTASIA, AND W. A. WELLS. 1971. Determination of arsenical herbicide residues in plant tissues. Weed Sci. 19: 412–416.

SEYDEL, I. S. 1972. Distribution and circulation of arsenic through water, organisms, and sediments of Lake Michigan. Arch. Hydrobiol. 71: 17–30.

THIEL, R., AND G. CARPENTER. 1970. Photometric determination of traces of arsenic in natural water. Bull. Centre Rech., Pau, Belgium. 4: 243.

Summerkill Risk in Prairie Ponds and Possibilities of its Prediction

JAN BARICA

Department of the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6

BARICA, J. 1975. Summerkill risk in prairie ponds and possibilities of its prediction. J. Fish. Res. Board Can. 32: 1283–1288.

Summer fish kills in shallow, landlocked ponds of the Erickson–Elphinstone area, southwestern Manitoba, were caused by collapses of heavy algal blooms, mostly *Alphanizomenon flos-aquae*, and subsequent oxygen depletion. Kills occurred only in ponds that were in the specific conductance range of 800–2000 μmho/cm and where chlorophyll *a* concentrations exceeded 100 μg/liter. A practical rating system for assessment of summerkill risk was suggested. Correlations between various parameters from 51 ponds were computed; the best correlation (r = 0.866; P = >0.99) was found between the late-winter concentration of ammonia nitrogen and the maximum concentration of chlorophyll *a* in the following summer. Two summerkill prediction systems were proposed, based on ammonia, dissolved oxygen, and Secchi disc transparency, enabling the prediction of summerkill risk 9 or 3 mo prior to stocking of the fish.

BARICA, J. 1975. Summerkill risk in prairie ponds and possibilities of its prediction. J. Fish. Res. Board Can. 32: 1283–1288.

Les mortalités estivales dans les étangs peu profonds et sans émissaires de la région Erickson–Elphinstone, sud-ouest du Manitoba, sont causées par les retombées d'abondantes floraisons algales, en grande partie d'*Aphanizomenon flos-aquae*, et à l'épuisement d'oxygène qui s'ensuit. Les mortalités ne se produisent que dans les étangs qui se trouvent dans les limites de conductance spécifique de 800–2000 μmho/cm et où les concentrations de chlorophylle *a* dépassent 100 μg/litre. L'auteur suggère un système de classement pratique de risque de mortalités estivales. Il a établi des corrélations entre les divers paramètres de 51 étangs; la meilleure corrélation (r = 0.866; P = >0.99) est celle qui existe entre la concentration de l'azote ammoniacal tard en hiver et la concentration maximale de chlorophylle *a* à l'été suivant. Il propose deux systèmes de prédiction, fondés sur l'ammoniaque, l'oxygène dissous et la transparence au disque de Secchi, permettant de prédire le risque de mortalités estivales 9 à 3 mois avant l'ensemencement des poissons.

Received August 19, 1974
Accepted March 21, 1975

Reçu le 19 août 1974
Accepté le 21 mars 1975

SUMMER fish kills are recognized to be a serious problem impeding the development of a trout farming industry in ponds of the Canadian prairies (Lawler et al. 1974). While summer fish farming in winterkill lakes (Johnson et al. 1970; Sunde et al. 1970) benefits from the naturally high fertility of these lakes, it is destroyed at advanced stages of eutrophication. In extreme cases, sudden collapses of algal blooms, followed by rapid decomposition of the dead algal cells and subsequent oxygen depletion, result in fish kills (Prescott 1959; Abeliovich 1969; Ayles and Lark 1975). Since practical methods for prevention of summerkills are not yet available, the best solution seems to be to avoid stocking lakes that pose a high summerkill risk. In view of the abundance of these small ponds in midwestern Canada (several hundred thousand) and possible financial losses when stocking improper lakes, this approach to dealing with the problem appears to be justified.

This paper is based on the results of extensive studies of 51 pothole lakes, published elsewhere (Barica 1975). Its objective is to present significant criteria for assessing and predicting the summerkill risk.

Printed in Canada (J3528)
Imprimé au Canada (J3528)

Characteristic Features of Prairie Ponds in the Study Area

The aquaculture study area is located in central Canada at about 50°30′N–100°10′W in the Erickson–Elphinstone district of southwestern Manitoba. The main resource base of the area is grain and cattle farming. About 52% of the land is cultivated. Thousands of marshes, sloughs, and pothole lakes occupy topographic depressions in this area. Only a few contain native fishes because of the high incidence of winterkill. Dissolved oxygen becomes totally depleted by late winter in most of the lakes for they are typically shallow and highly fertile; winters are long and ice and snow cover is thick. Many invertebrates such as small crustaceans and insect larvae, however, are able to survive in the winterkill conditions with the result that these lakes are extremely rich in fish food organisms. Experiments were initiated in 1968 to test the utility of this resource for the commercial production of rainbow trout (Lawler et al. 1974). Most of the lakes are landlocked. Of 71 lakes that have been experimentally stocked with rainbow trout since 1968, only 6 are known to have an intermittent surface outflow. A total of 69.5% of them were 1–3.9 m deep (maximum depth), with highest frequency in the interval of 2–2.9 m (36.2%). None of them showed a normal pattern of thermal stratification, forming a distinct epi- and hypolimnion. Only in two relatively deep lakes (maximum depth 4.9–5.8 m, lakes 302 and 154) a partial thermocline appeared at a depth of about 4–5 m. Summer temperatures of all lakes shallower than 4 m fluctuated within 1–3 C between the surface and the bottom. These ponds can be classified, therefore, as thermally unstratified, or perhaps polymictic lakes.

The experimental lakes varied greatly in salinity and ionic composition. Concentration of total ions varied from 268 to 9720 mg/liter (305–7840 μmho/cm as specific conductance), with 52.7% of the total in the 1000–2000 μmho/cm range. A total of 44.4% belonged to the true SO_4-Mg type; 17.7% to the intermediate SO_4-HCO_3, Mg type; 11.1% to the intermediate SO_4-HCO_3, Mg-Ca type; and the remaining 27.8% represented various intermediate and mixed types.

The aquaculture experimental lakes are representative of hundreds of thousands of similar winterkill lakes in the Canadian prairies that are potentially suitable for fish farming. More information on a general description of the physical character of the experimental area and the lakes it contains is given in a separate report (Sunde and Barica 1975).

Nutrient cycling and regeneration during a year in some selected ponds were described elsewhere (Barica 1974, 1975). These studies demonstrated that the major release of nutrients, namely NH_3-N and soluble reactive phosphorus (SRP), takes place regularly in late winter during anoxic conditions under the ice (February to early March) and remains without substantial change for this period. The release is noticeable in nonsummerkill lakes; however, in the summerkill lakes its magnitude is 2–3 times greater. In summer, nonsummerkill lakes show relatively uniform chlorophyll *a*, nutrient, and dissolved oxygen levels, while in summerkill lakes they oscillate, with chlorophyll *a* exponentially increasing to over 100 μg/liter within 1–2 wk. This is followed within one to several weeks by a sudden collapse of the algal population. The summer chlorophyll *a* peak is not a regular phenomenon for different lakes and can take place any time between late May and early September. The algal collapse is always preceded by a peak in the chlorophyll *a* level and DO concentration, and consequently, the minimum Secchi disc transparency and nutrient levels. It is the maximum or minimum values of various parameters (nutrients, chlorophyll *a*, Secchi depth, DO, etc.) that characterize the status of the lakes, rather than average values which are meaningless. In a given lake, these extremes reach similar levels annually at about the same time; the lakes generally do not show any substantial change in their maximum biomass from one year to another.

Summerkill Risk Rating

From analysis of results from 51 pothole lakes (Barica 1975) the following conclusions can be drawn:

1) Summerkill, whether total or partial, occurred in ponds that exceeded summer maximum of chlorophyll *a* of 100 μg/liter. This does not mean, however, that the algal blooms at this level must necessarily collapse; there were many instances where the *Aphanizomenon flos-aquae* bloom survived even at higher chlorophyll *a* concentrations (see Fig. 2). Although the summerkills caused by collapses of the *A. flos-aquae* blooms were the most typical and frequent in our study lakes, in 1973 there were some cases of summerkills caused by other blooms, namely mixture of *Microcystis*, *Merismopedia*, and diatoms (Lake 154, late June), or *Microcystis* and *Anabaena* (Lake 879, June) or even diatoms and green algae (Lake 103, late May; Kling 1975). In all these cases, the 100 μg/liter level of chlorophyll *a* was also surpassed. Secchi disc transparencies in these lakes were less than 0.4 m prior to the summerkill.

2) Prairie ponds with chlorophyll *a* summer maxima between 25–100 μg/liter developed only moderate, however, visible blooms (Secchi disc transparency 0.5–1 m) and usually contained *Anabaena* and *Microcystis* blooms, or diatoms in spring. None of these ponds have exhibited summerkill so far.

3) Ponds with chlorophyll *a* maxima less than 25 μg/liter were usually clear, without visible blooms, and with Secchi readings often down to the bottom. However, they frequently developed dense growths of bottom vegetation.

These arbitrary limits make possible a practical division of prairie ponds into two groups: low summerkill risk lakes (chlorophyll *a* <100 μg/liter) and high summerkill risk lakes (chlorophyll *a* >100 μg/liter), with possible finer subdivisions to low, medium, high, and very high risk lakes, as shown in Table 1. If necessary, the chlorophyll *a* limits can be substituted for practical fish farmers' use by measuring Secchi disc transparency only, using the graph shown in Fig. 1. Although rough, this value can play a major role in a year-to-year assessment of the summerkill risk by farmers themselves.

TABLE 1. Frequency distribution of different chlorophyll *a* ranges (summer maxima) in aquaculture experimental lakes and summerkill risk rating.

Chlorophyll *a* range (μg/liter)	No. of lakes	% of total	Predominant algae species (midsummer)[a]	Secchi disc. transp. (*m*)	Appearance	Summerkill risk[b]	
0–25	13	25.5	*Microcystis* *Merismopedia* *Ceratium*	>1.0	clear, no blooms frequent macrophytes	low	LOW
25–100	21	41.2	*Anabaena* *Microcystis*	0.4–1.0	moderate blooms	medium	
100–200	10	19.6	*Aphanizomenon flos-aquae*	<0.4	dense colonies, clumping, scums	high	HIGH
>200	7	13.7				very high	

[a] (Kling 1975).

[b] Arbitrary limits and categories based on data published separately (Barica 1975).

Parameters for Summerkill Risk Prediction

Series of regression analyses were performed on the data from experimental lakes to determine the best model relating maximum chlorophyll *a* concentration to the following dependent variables (w = winter, s = summer):

For lake water:

max. NH$_3$–N (w,s); max SRP (w,s); max. TDN, TDP[1] (w,s); max. DON, DOP, DOC (w,s); min. DO (s); max. DO (w); min. Secchi disc transparency (s); E$_h$ (w); specific conductance (s).

For lake sediments:

NH$_3$–N (w, interstitial water); SRP (w, interstitial water); IOD (w) BOD$_1$ (w); E$_h$ (w).

All correlated parameters, which showed the highest significance levels, are summarized in Table 2, together with the data on duration of their occurrence.

Figure 2 shows the best correlation of all obtained, namely between winter maximum of NH$_3$–N in lake water and the maximum chlorophyll *a* in the next summer. This relationship seems to be promising for predictive purposes and also confirms previously determined limits for high summerkill risk (about 100 μg/liter chlorophyll *a*), as all summerkill lakes are distributed over this value.

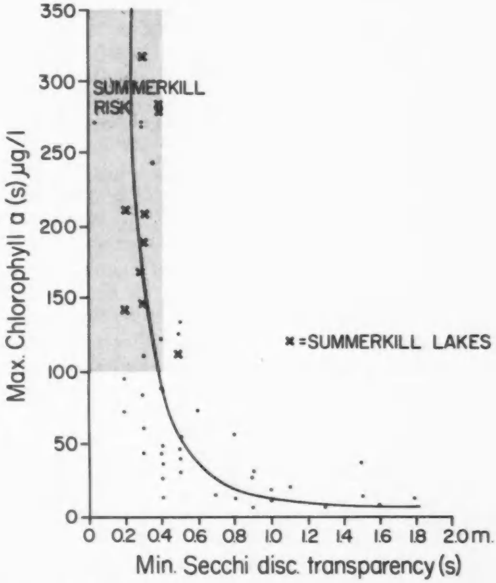


FIG. 1. Relationship between the maximum chlorophyll *a* and minimum Secchi disc transparencies in various prairie ponds (Erickson–Elphinstone district of southwestern Manitoba). For *r* values and regression equations see Table 2.

Figure 3 presents an inverse correlation between the summer chlorophyll *a* maxima and mean summer specific conductance. All summerkill lakes are distributed in the range of about 800–2000 μmho/cm. However, they represent only about one third of all lakes distributed in this range, with the rest of them being all nonsummerkill lakes. This specific conductance range cannot therefore be excluded from stocking programs for practical reasons. More experimental work, now in progress, is needed to clarify this.

---

[1] TD = total dissolved; DO (N,P,C) = dissolved organic (N,P,C); DO = dissolved oxygen; E$_h$ = redox potential; IOD = immediate oxygen demand; BOD = biochemical oxygen demand. For the methods see Barica 1975.

TABLE 2. Significant parameters[a] (x) for prediction of summerkill risk. w = winter, s = summer, y = max. chlorophyll *a*(s).

Parameter (x)	Lower limit for high summerkill risk	Period of occurrence[b]	Duration of occurrence	Correlation coefficient (*r*)	Regression equation
Max. NH_3–N(w) water	1000 µg/liter	late winter (Feb.)	4–6 wk	0.866	y = 0.108x − 18
Max. NH_3–N(s) water	600–800 µg/liter	all summer (May–Sept.)	3–10 days	0.570	y = 0.091x + 52
NH_3–N(w) sediments (interst. water)	7–8 mg/liter	late winter	4–6 wk	0.554	y = 10.9x − 1.2
Max. TDN(s) water	3500 µg/liter	late summer (Aug.–Sept.)	3–4 wk	0.466	y = 0.03x + 23
Max. DON(s) water	3500 µg/liter	late summer	3–4 wk	0.383	y = 0.025x + 3
E_h(w) sediments	−100 mV	late winter	4–6 wk	−0.636	y = −0.88x − 56
Max. DO(s) water (daylight)	13–15 mg/liter	all summer	1–3 days	0.619	y = 14.8x − 94
Min. DO(s) water (daylight)	4 mg/liter	all summer	1–6 days	−0.629	y = −22.8x + 209
Min. DO(w) water	1 mg/liter	late winter	4–6 wk		—[c]
Max. chlorophyll *a*(s) water	100 µg/liter	all summer	1–3 days		—[c]
Min. Secchi disc transparency	0.3 m for non-*Aphanizomenon flos-aquae* bloom	all summer	1–3 wk	−0.762	$y = -21.1x^{-1.39}$
	0.4 m for *Aphanizomenon flos-aquae* bloom	all summer	1–3 wk		
Spec. conductance(s)	800–2000 µmho/cm (range; no limit set)	all summer	4–5 mo	−0.243	y = −0.024x + 129

[a] 1% level of significance for water, 5% level for the sediments and specific conductance (Snedecor and Cochran 1967).
[b] i.e. anytime in that period.
[c] Based on Tab. iii, Barica 1975.

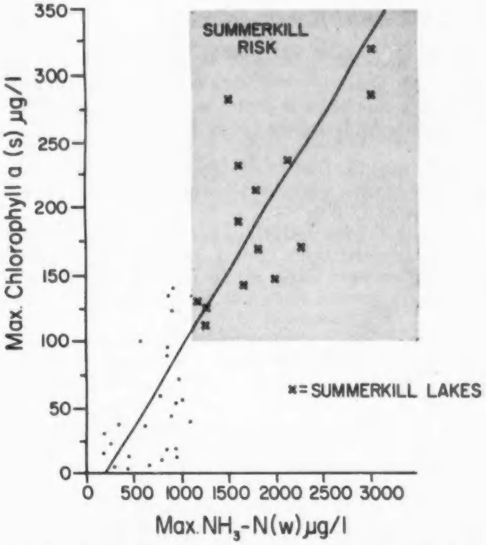


FIG. 2. Correlation between the maximum summer chlorophyll *a* concentration and the maximum ammonia in the previous winter (February to early March) in various prairie ponds (Erickson–Elphinstone district of southwestern Manitoba). For *r* values and regression equations see Table 2.

Considering the significant parameters from Table 2 for lake water only and excluding TDN, DON, and those for lake sediments because of their analytical complexity and lower significance, two possible systems of summerkill prediction emerge as follows:

1) *Summer-to-summer predictions* (9 mo prior to stocking): This would involve obtaining maximum chlorophyll *a* values for each particular lake, with supplementary information on maximum and minimum DO, and Secchi disc transparency in the summer 1 yr prior to intended planting. Fish stocking should be confined to lakes of maximum summer chlorophyll *a* concentration below 100 µg/liter and DO in the range 6–15 mg/liter. Secchi disc transparency should exceed 0.4 m for *Aphanizomenon flos-aquae* blooms and 0.3 m for other blooms.

2) *Winter-to-summer predictions* (3 mo prior to stocking): This system would require only obtaining the late-winter (February to early March) NH_3–N concentration with supplementary data on dissolved oxygen.

Lakes with maximum NH_3–N concentration exceeding 1000 µg/liter should be avoided for fish farming, as well as the lake having winter minimum DO concentrations higher than 1 mg/liter (complete anoxic conditions in the winter are desirable for this kind of summer fish farming, as mentioned elsewhere (Johnson et al. 1970; Sunde et al. 1970).

Although the summer-to-summer prediction seems to be more reliable, it is difficult as it requires a regular monitoring of potential lakes over the whole summer, since the parameter maxima can be reached any time within the span of several months. The probability of missing the maximum is fairly high and the sampling coverage to avoid it extensive (perhaps weekly intervals).

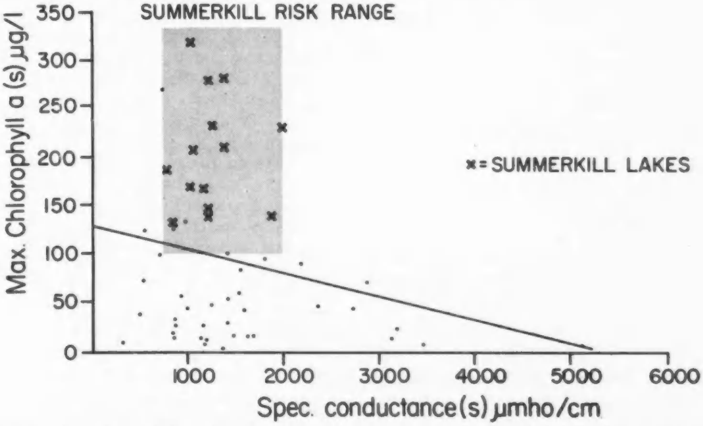


FIG. 3. Correlation between summer maximum of chlorophyll *a* and specific conductance (mean summer values) in various prairie ponds (Erickson–Elphinstone district of southwestern Manitoba). For *r* values and regression equations see Table 2.

On the other hand, the winter maxima of NH_3 and minima of DO are reached regularly in February to early March and remain there for several weeks. Their detection is therefore much more reliable.

Both summerkill prediction systems are designed for prairie pothole lakes of moderate salinity and landlocked character, for which the Erickson–Elphinstone district is representative.

Discussion

There have been several attempts recently to predict quantitatively aquatic production on the basis of some environmental parameters (Vollenweider 1968; Hrbáček 1969; Serruya and Pollingher 1971; and others). However, the Canadian prairie ponds differ substantially from most of the "normal" stratified lakes due to their extreme shallowness, landlocked character, lack of permanent surface inflow and outflow to estimate nutrient loading, long freeze-up, and regular winter oxygen depletion. They tend to accumulate the allochthonous material from their agricultural drainage basins as its removal via groundwater seepage is slow. It might seem surprising that the best correlations with chlorophyll *a* were found for nitrogen. This is presumably due to its high rate of accumulation from the atmosphere as a result of N-fixation by blue-green algae, which was found to be extremely high in our ponds (as much as 0.9 g/m^2 per day in Lake 885; Flett personal communication). This explains also high concentrations of dissolved organic nitrogen, which is known to be produced by algae (Fogg 1971). The maximum winter ammonia concentration, which is reached regularly in late winter, represents an initial starting supply of nitrogen for the upcoming productive season, and determines to great extent the magnitude of algal biomass in the following summer.

The two proposed prediction systems (9 and 3 mo prior to intended stocking) are subject to verification and improvements. They are currently being tested on other prairie ponds. There are still several factors that should be clarified in follow-up studies: e.g. in the case of extremely shallow lakes (less than 1.5 m) that favor growth of macrophytes, chlorophyll *a* values obtained from seston do not represent the actual plant population. The effect of salinity on fish yields should also be elucidated. This paper is only a partial contribution to the overall problem of the suitability of prairie ponds for summer trout farming, of which the summerkill problem is an important part.

Acknowledgments

I am indebted to Dr G. B. Ayles, Dr F. P. Healey, and L. A. Sunde for assistance and critical comments. H. Kling supplied the phytoplankton data. Diagrams were made by L. Davies and S. T. Zettler.

ABELIOVICH, A. 1969. Water blooms of blue green algae and oxygen regime in fish ponds. Verh. Int. Verein. Limnol. 17: 594–601.

AYLES, G. B., AND J. G. I. LARK. 1975. Summer mortality of rainbow trout (*Salmo gairdneri*) in Canadian pothole lakes. Paper presented to Canada Society of Environmental Biologists Annual Meeting, January 8–9, 1975, Vancouver, B.C.

BARICA, J. 1974. Some observations on internal recycling, regeneration and oscillation of dissolved nitrogen and phosphorus in shallow self-contained lakes. Arch. Hydrobiol. 73: 334–360.

1975. Geochemistry and nutrient regime of saline eutrophic lakes in the Erickson–Elphinstone district of southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 511: 82 p.

FOGG, G. E. 1971. Extracellular products of algae in freshwater. Arch. Hydrobiol. Beih. 5: 1–25.

HRBÁČEK, J. 1969. Relations between some environmental parameters and the fish yields as a basis for a predictive model. Verh. Int. Verein. Limnol. 17: 1069–1081.

JOHNSON, L., G. H. LAWLER, AND L. A. SUNDE. 1970. Rainbow trout farming in central Canada. Fish. Res. Board Can. Tech. Rep. 165: 18p.

KLING, H. 1975. Phytoplankton successions and species distribution in prairie ponds of the Erickson–Elphinstone district, southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 512: 31 p.

LAWLER, G. H., L. SUNDE, AND J. M. WHITAKER. 1974. Trout production in prairie ponds. J. Fish. Res. Board Can. 31: 929–936.

PRESCOTT, G. W. 1959. Biological disturbances resulting from algal populations in standing waters. Proc. Pymatuning Symp. Ecology: The ecology of algae. Univ. Pittsburg Pymat. Lab. Spec. Publ. 2: 22–30.

SERRUYA, C., AND V. POLLINGHER. 1971. An attempt at forecasting the *Peridinium* bloom in Lake Kinneret (Lake Tiberias). Mitt. Int. Ver. Theor. Angew. Limnol. 19: 277–291.

SNEDECOR, C. W., AND W. C. COCHRAN. 1967. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, Iowa. 593 p.

SUNDE, L., AND J. BARICA. 1975. Geography and lake morphometry of the aquaculture study area in the Erickson–Elphinstone district of southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 510: 35 p.

SUNDE, L. A., J. WHITAKER, AND G. H. LAWLER. 1970. Rainbow trout production in winterkill lakes. Proc. Symp. Management Midwest Winterkill Lakes. Spec. Publ. Am. Fish. Soc.: 57–63.

VOLLENWEIDER, R. A. 1968. Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors of eutrophication. Organization for Economic Cooperation and Development Rep. DAS/SST 68.27. 159 p.

Characterization and Subcellular Localization of Leucine Aminonaphthylamidase (LAN) in Rainbow Trout (*Salmo gairdneri*)

G. R. Bouck
Western Fish Toxicology Station (EPA), Corvallis, Oreg. 97330, USA

P. W. Schneider Jr.
River Basins Studies, U.S. Fish and Wildlife Service, Portland, Oreg. 97208, USA

Janet Jacobson
University of Oregon Medical School, Portland, Oreg. 97403, USA

and R. C. Ball
Department of Fisheries and Wildlife, Michigan State University, East Lansing, Mich., USA

Bouck, G. R., P. W. Schneider Jr., J. Jacobson, and R. C. Ball. 1975. Characterization and subcellular localization of leucine aminonaphthylamidase (LAN) in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 1289–1295.

LAN analyses appear to have diagnostic value in fish pathobiology and studies were undertaken to determine optima for substrate concentration, pH, reaction time, temperature, and buffer ions. Citrate ion did not inhibit LAN at anticoagulant levels, but cyanide, pyrophosphate, and EDTA had an inhibitory effect. Storage of samples at —10 and 1 C resulted in small but significant reductions of LAN activity, while at room temperature enzyme activity was rapidly lost. LAN activity was distributed among liver fractions as follows: microsomes, 12%; mitochondria, 9%; cellular sap, 37%; other, 50%. Three isozymes of LAN were found. Blood plasma contained significant amounts of LAN activity which was significantly higher in cold- than in warm-acclimated fish. However, these LAN levels were comparable when their activity was extrapolated to body temperatures.

Bouck, G. R., P. W. Schneider Jr., J. Jacobson, and R. C. Ball. 1975. Characterization and subcellular localization of leucine aminonaphthylamidase (LAN) in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 1289–1295.

Le dosage de la leucine amino naphthylamidase (LAN) semble avoir une valeur diagnostique dans la pathobiologie des poissons, et des études furent entreprises dans le but de déterminer les conditions optimales de concentration du substrat, pH, temps de réaction, température et ions tampons. L'ion citrate n'inhibe pas la LAN à des niveaux anticoagulants, mais le cyanure, le pyorphosphate et l'EDTA ont un effet inhibiteur. L'entreposage des échantillons à —10 et 1 C entraîne des réductions faibles mais significatives d'activité de la LAN, alors qu'à la température ambiante, l'activité de l'enzyme disparaît rapidement. L'activité de la LAN est répartie comme suit dans les fractions du foie: microsomes, 12%; mitochondries, 9%; liquide cellulaire, 37%; autre, 50%. Nous avons trouvé trois isozymes de la LAN. Le plasma sanguin renferme des quantités significatives d'activité de LAN, nettement plus élevées chez les poissons acclimatés au froid qu'à la chaleur. Cependant, ces niveaux de LAN sont comparables quand leur activité est extrapolée par rapport aux températures du corps.

Received September 26, 1974
Accepted March 21, 1975

Reçu le 26 septembre 1974
Accepté le 21 mars 1975

Enzymes in blood have been used successfully as measures of health among humans and other mammals (Hess 1963; Lawrence 1964; Wilkinson 1965), but the value of this approach remains relatively unexplored for piokilotherms. For example, fish have an array of enzymes similar to those in humans (Tarr 1969), and damage to tissues in fish can produce a net transfer of cellular enzymes to the interstitial lymph and thence into the blood (Bouck 1966). But the use of many clinical tests for enzymes requires the presumption that the assay procedures, biochemical properties, organosomatic distribution, and clinical significance are equivalent between homeothermic terrestrial mammals and poikilothermic fish. We decided to investigate this presumption and selected L-leucine-β-naphthylamidase (LAN) for study. LAN was selected because it appeared to be stabile at room temperature, it has

Printed in Canada (J3580)
Imprimé au Canada (J3580)

chromogenic substrates for isozyme analyses, and its assay procedures are simple and easy. Furthermore, LAN has been used to evaluate a variety of stresses including liver damage (Smith et al. 1965), vitamin deficiency (Cheeseman et al. 1967), wasting disorders (Hess 1963; Lawrence 1964), allergic responses (Innerfield et al. 1964; Rabb 1966), and other stresses. Therefore, we experimented with the basic assay method, adapted it to rainbow trout (*Salmo gairdneri*), and herein report some of the properties of LAN, including its subcellular distribution, its isozymes, and activity levels in blood.

LAN has been called leucine amino peptidase (LAP, 3.4.1.1) because it can hydrolyze a variety of L-leucyl terminal amides on other peptide moieties (Hill and Smith 1956). Also, LAN has been called "amino acid naphthylamidase" (Smith et al. 1965), but Smith and Rutenburg (1966) reported that LAP and LAN may be distinctly different enzymes. Whether or not this is the case and what impact it would have on clinical procedures or interpretation is uncertain. Literature surveys reveal an abundance of information on LAP (Johnson and Berger 1942; Smith and Hill 1960; and Delange and Smith 1971), but essentially nothing to clarify the status of LAN in salmonid fish. Because of this conflict and paucity of data, it seems appropriate to omit further references at present. Indeed, this confusion emphasized the need to investigate the characteristics of LAN in rainbow trout prior to a proposed study of environmental stress.

Methods

Rainbow trout were adjusted to laboratory conditions for at least 2 wk prior to their use and were fed a balanced ration of Oregon Moist Pellets II ad lib. The fish were maintained at about 12 C in carbon filtered, soft tap water. Photoperiod was not controlled. Total body length varied from about 15 to 25 cm. Immediately prior to their use, the fish were euthanized with tricane methane sulfonate (M.S. 222).

Biochemical studies were performed on liver extract prepared by combining 1 vol of liver with 2 vol of cold 0.25 M sucrose, followed by tissue disruption in cold glass mortar and teflon pestle. The resulting slurry was centrifuged at 0 C for 90 min at 40,000 × *g*. The liquid portion was drawn off and diluted about 1:100 with distilled water. This diluted sample contained about 0.3% liver and constituted the liver extract for most of these analyses.

One milliliter of the above liver extract or 50 μl of plasma diluted to 1 ml were analyzed using the standard method of Goldbarg and Rutenburg (1958). A unit of LAN activity was equivalent to the liberation of 1.0 μg of β-naphthylamine/h at 25 C. However, assay conditions were varied to allow an assessment of indicated parameters, and for purposes of demonstrating the optima or relative effect, LAN activity was usually expressed as a percentage of the maximum activity observed in a given test series. This is because the LAN activity of liver extract varied from 2.4 to 9.3 units/ml between extracts from different fish.

The experimental error associated with the standard LAN assay was estimated by analyzing eight subportions of liver extract. The resulting LAN activity averaged 6.84 units and ranged from 6.00 to 7.16 units with a standard deviation of 0.17 units. Collateral testing established that the resulting LAN activity in a sample was not influenced significantly by mechanical stirring, shaking, or quiescence during the incubation period.

The distribution of LAN activity among liver cell components was investigated via centrifugation according to Geise (1962). LAN activity was determined as above and was adjusted to account for the activity of the whole fraction and tissue.

Isozymes of LAN were studied in vertical slabs of 5% polyacrylamide gel, using a vertical electrophoresis and technique reported by Bouck and Ball (1968). After electrophoresis LAN isozymes were detected by the method of Lawrence (1964). Chromogenic development of LAN isozymes were followed over a 4-h period. The zymogram was recorded graphically by measuring the migration disturbance of a given isozyme and comparing it to that of bromophenol-blue labeled, human serum albumin. Control zymograms contained no substrate, but did develop some off-color spots which were discounted.

Levels of LAN in fish blood were studied in rainbow trout that were held in moderately hard water as described by Bouck and Ball (1965). After arriving at the laboratory, fish were randomly assigned to two different holding systems where different temperatures could be developed and maintained. After an initial week of observation at 13 C, the water temperatures were raised or lowered, respectively, by about 3 C/day until one system had reached 7 C and the other had reached 17 C. Exposure to these temperatures continued for 21 days and fish food pellets were offered ad lib. each day. Photoperiod was not controlled.

Blood samples were collected and analyzed for hemoglobin, hematocrit, and plasma protein using methods described by Bouck and Ball (1966); LAN was determined as before.

Results and Discussion

REACTION KINETICS

Total LAN activity increased linearly with reaction time, and the hydrolysis of L-leucyl-β-naphthylamide by LAN, therefore, follows zero order kinetics through a 100-min period. This demonstrates that the substrate concentration of this medium had been maintained at a level so that only the enzyme concentration was limiting.

Temperature Dependency

Maximum LAN activity occurred at about 55 C. Above this LAN activity diminished rapidly, losing about 95% of its activity in the range of 60–70 C, and it lost all of its activity upon reaching 100 C. Thus, the temperature for LAN's maximum activity (optimum temperature) is considerably above the lethal temperature of rainbow trout.

The relationship between temperature and enzyme activity was linear in the lower temperature range. However, one should not confuse the activity levels at the standard assay temperature (25 C) with activity levels at body temperature (typically less than 15 C).

Buffer and pH Dependency

Four buffer systems were tested individually at 0.1 M and pH 7.5. Tris and Tris-maleate buffers produced the highest levels of LAN activity. Phosphate and Tris-EDTA-borate buffer systems resulted in LAN activity levels that were consistently about 10% lower activity than when tested in Tris buffer.

Using Tris buffer, the effect of pH upon LAN activity was determined and is depicted in Fig. 1. LAN activity reached a maximum at about pH 8.0 and diminished rapidly above and below this point. However, the solubility of L-leucyl-β-naphthylamide diminishes rapidly above pH 8.0; hence, we recommend holding the incubation medium at about pH 7.8–8.0. Otherwise, the reaction could become rate limited by insufficient dissolved substrate.

Other authors have reported pH optima for LAP ranging from pH 6.8–7.2 in humans (Smith et al. 1965; Goldburg and Rutenburg 1958) to pH 7.8–9.3 in rats (Smith et al. 1952).

Effects of Sample Storage on LAN Activity

LAN activity was determined as functions of storage time and storage temperature as depicted in Fig. 2. Freezing to −10 C for either 1 or 5 days resulted in about 10% less LAN activity than in the initial sample. Storage at 1 C for 1 day resulted in 25% less LAN activity and this loss extended to 62% in 5 days of storage. However, storage at 19 C for only 1 day resulted in a 75% reduction of LAN activity. Thus, LAN was significantly labile when frozen as was reported by Patterson et al. (1963). Delange and Smith (1971) reported that LAP is stable indefinitely when frozen with $MgCl_2$ between pH 7–9.

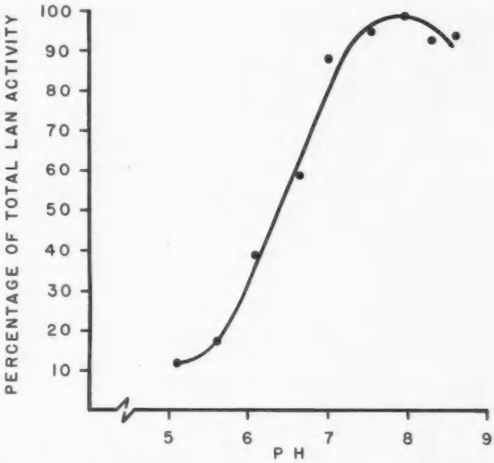


FIG. 1. Influence of pH upon L-leucyl-β-naphthylamidase (LAN) activity from liver of rainbow trout (*Salmo gairdneri*).

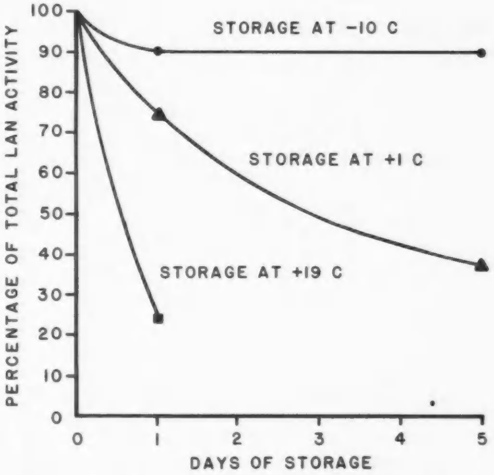


FIG. 2. Effects of storage on the activity of liver L-leucyl-β-naphthylamidase from rainbow trout.

Possibly tissue or blood samples are more stable than liver extract, but regardless, it seems unwise to subject samples to any unnecessary storage, unless such storage can be shown to have no significant effect.

Inhibitory Effect of EDTA, Citrate, Pyrophosphate, and Cyanide

EDTA was added in concentrations ranging from 0.15 mM. LAN activity decreased 10% in the medium with 1 mM EDTA added and this reached 15% with the addition of 15 mM EDTA.

This observation is in poor agreement with the results of Burstone and Folk (1956), and Smith et al. (1965), who reported stronger inhibition of mammalian LAP by 5 mM EDTA.

Sodium citrate was tested at concentrations ranging from 0 to 10 mM and no depression of LAN activity was observed. Citrate is, therefore, considered acceptable for use as an anticoagulant where LAN is under study. However, it should be noted that Smith (1948) reported a variable effect of citrate upon LAP in skeletal, heart, and uterine muscle.

When sodium cyanide and sodium pyrophosphate were tested in duplicate at concentrations ranging from 0 to 10 mM, LAN activity decreased progressively with increased cyanide or pyrophosphate concentration (Fig. 3). Cyanide may be a slightly more effective inhibitor to trout LAN than pyrophosphate, but neither results in a 60% inhibition at 0.01 M as reported by Burstone and Folk (1956). We do not know if a depression in LAN activity could result from environmental exposure to sublethal levels of cyanide.

Effects of Heavy Metals on LAN Activity

An attempt was made to determine if heavy metals (mercury, cadmium, and copper) influenced LAN activity as reported for LAP by Smith et al. (1965) and Delange and Smith (1971). Additions of 1.0 mM of a given metal precipitated the protein in liver extract and the result was essentially total inhibition of LAN activity. This result indicates that a sulfhydryl (—SH) group(s) may be associated with the active site of the enzyme, but we do not imply that metal exposure in vivo will necessarily accomplish this result.

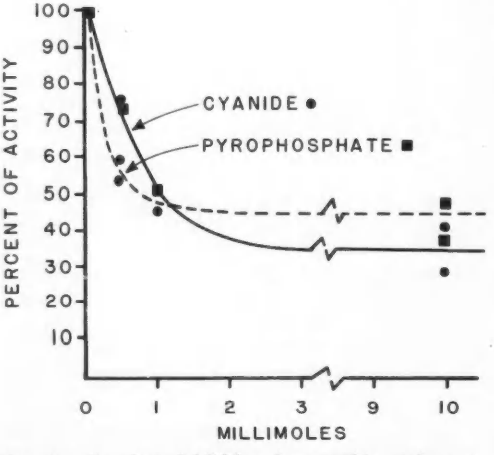


FIG. 3. In vitro inhibition by cyanide and pyrophosphate of L-leucyl-β-naphthylamidase from liver of rainbow trout.

Distribution of LAN Activity in Hepatic Cell Fractions

About 50% of the total LAN activity and about 20% of the initial tissue volume was found in the fraction sedimented by 1200 × *g* for 10 min. Fraction I appears to consist of whole cells, membranes, nuclei, and lysosomes.

Fraction II was sedimented after the above, plus 10 min at 5000 × *g*, and consisted mainly of mitochondria. This sediment fraction contained essentially no LAN activity.

Fraction III was sedimented by 40,000 × *g* for 90 min and consisted mainly of microsomes. This fraction had about 12% of the total LAN activity.

Fraction IV was the unsedimented liquid after the above centrifugation, and contained LAN in apparently soluble form. This fraction contained about 37% of the total LAN activity and about 65% of the initial tissue volume.

Smith et al. (1965) conducted a similar study on human liver; LAP was found in all fractions, but was found mainly in the 1500 × *g* fraction. Patterson et al. (1963) reported 45% of the LAN activity in the soluble fraction of mouse acites cells. Felgenhauer and Glenner (1966b) reported differential effects of inhibitors on soluble and particle-bound LAN in rat kidney.

Our results agree with the finding of a considerable amount of LAN activity in the cellular sap of liver. If the liver should become damaged for whatever reasons, LAN would be expected to leak into the blood directly or into interstitial space, and then pass via the lymphatic system to enter the blood, thusly, elevating the plasma–LAN (P–LAN) activity.

Isozymes of LAN

Three fractions of LAN were observed in rainbow trout (Fig. 4). LAN fraction I (LAN-I) migrated about 65%, and LAN II migrated 35% of the distance traveled by human serum albumin during electrophoresis. LAN-III was iso-electric or nearly so. Both LAN I and II had bands about twice the width of the albumin fraction; this may indicate further molecular heterogeneity. LAN-III was a sharply defined, narrow band. Possibly other isozymes were present, but if so, they carried a positive net charge (+) or otherwise could not migrate into the gel. Use of other gels or buffers at a different pH may resolve still further isozymes of LAN.

LAN-I migrated faster and was present in blood

TABLE 1. Summary of the effects of two temperature regimes on plasma leucine aminonaphthylamidase and other blood parameters of rainbow trout (*Salmo gairdneri*).

						Leucine amino-naphthylamidase[a]	
	Total length (*cm*)	Weight (g)	Hemoglobin (g/100 ml)	Hematocrit (Packed cell volume/ 100 ml)	Plasma protein (g/ 100 ml)	(Units/ml of plasma)	(Units/g of plasma protein)
Held at 17 C (n = 8)							
Mean	22.6	118.2	5.6	31.8	2.24	220.3	98.6
95% limit	±0.82	±12.28	±0.51	±4.10	±0.51	±51.98	±9.10
Coefficient of variation	0.05	0.16	0.22	0.19	0.34	0.35	0.14
Held at 7 C (n = 7)							
Mean	21.0	91.7	5.1	31.4	2.21	300.9[b]	136.8[b]
95% limit	±1.61	±22.49	±0.58	±7.69	±0.24	±50.46	±21.13
Coefficient of variation	0.10	0.33	0.15	0.33	0.15	0.23	0.21

[a] One unit of activity is the hydrolysis of a microgram of leucyl-β-naphthylamide per hour (assayed at 25 C).
[b] Significantly different at 0.1 level.

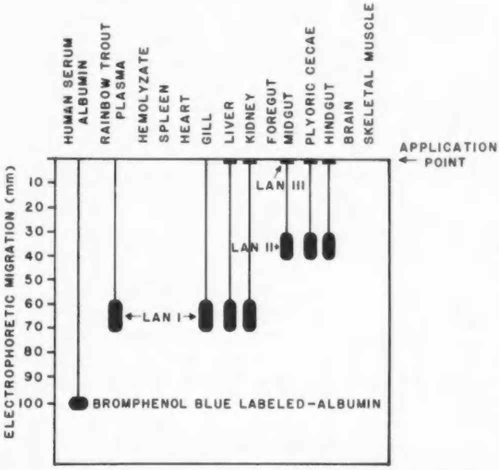


FIG. 4. Zymogram of L-leucyl-β-naphthylamidase (LAN) from various tissues of rainbow trout.

plasma, gill, liver, and kidney. On the other hand, LAN-II was present in midgut, pyloric caecae, and hindgut, while LAN-III was present in liver, kidney, midgut, pyloric caecae, and hindgut. LAN activity was not evident in detectable amounts, if any, in the fractions of hemolyzate, spleen, heart, foregut (stomach), brain, or muscle. Smith and Rutenburg (1963) reported tissue specific LAN isozymes in human tissues and serum. However, Law (1967) reported that chicken LAN-I could be transformed into the slower migrating LAN-II by the enzymatic removal of sialic acid residues with neuraminidase.

These results indicate that electrophoretic analysis of trout plasma for LAN isozymes might identify the location of tissue damage either by environmental stress, toxicity, infection, or other trauma. One can speculate that increased levels of LAN-I in the blood plasma might result from damage to gill, liver, or kidney. The absence of LAN-III in the same blood sample would tend to eliminate gills as the source since both liver and kidney contain LAN-III. But, if only LAN-II and III were in blood plasma, then the intestinal tract would be the indicated source. While this approach is relatively unexplored in fish pathobiology, it seems promising thus far.

PLASMA LAN AND EFFECTS OF ENVIRONMENTAL TEMPERATURE

Significant amounts of LAN activity were found in the blood plasma of apparently normal rainbow trout, and the level of plasma–LAN (P–LAN) activity was influenced by their environmental, hence body temperature (Table 1). P–LAN activity, when assayed at 25 C, was significantly higher among cold acclimated fish than among warm acclimated fish. On the other hand, no significant differences were evident between the cold- and warm-acclimated fish relative to their total length, body weight, total hemoglobin, hematocrit, or total plasma protein. Possibly P–LAN is more easily influenced by environmental factors than hemoglobin, hematocrit, or total plasma protein.

TABLE 2. Coefficients of correlation between leucine aminonaphythlamidase and other physiological variables of rainbow trout that were held 14 days at 7 or 17 C.

	Total length	Total body weight	Hemoglobin concn	Packed cell volume	Plasma protein concn	LAN per ml plasma	LAN activity per gram plasma protein
17 C (n = 8)							
Total length		+0.96	−0.23	−0.38	+0.45	+0.51	+0.36
Total body weight			−0.32	−0.54	+0.47	+0.52	+0.30
Hemoglobin concentration				+0.74[a]	−0.84[a]	−0.71[a]	+0.27
Packed cell volume					−0.70	−0.62	−0.02
Plasma protein concentration						+0.92[a]	−0.06
LAN activity per ml plasma							+0.33
7 C (n = 7)							
Total length		+0.98	+0.06	+0.22	+0.06	−0.38	−0.47
Total body weight			−0.04	+0.20	−0.02	−0.46	−0.51
Hemoglobin concentration				+0.08	−0.01	+0.63	+0.68
Packed cell volume					+0.14	−0.04	−0.17
Plasma protein concentration						+0.41	−0.23
LAN activity per ml plasma							+0.79

[a] Statistically significant at 0.1 level.

Correlation analyses were performed between each parameter for the 7 and 17 C acclimated fish, and the results are given in Table 2. A significant correlation existed between P–LAN activity and total hemoglobin among 17 C fish ($r = 0.63$) and among 7 C fish ($r = 0.71$). Also, P–LAN activity per milliliter of plasma was strongly and significantly correlated with the plasma protein concentration among 17 C fish ($r = 0.92$), but this was not the case at 7 C ($r = 0.41$).

It is imperative to distinguish between LAN activity levels at body temperatures and at standard assay temperatures. Because LAN activity was shown to be linear over the range of 5–25 C, we extrapolated from the P–LAN activity at 25 C to its estimated activity at its respective body (and environmental) temperature. When this adjustment was made, the P–LAN activity levels that were dissimilar at 25 C, became very similar at 7 and 17 C for respective groups. Possibly this indicates that a homeostatic mechanism exists and maintains a relatively constant P–LAN activity at a given body temperature. But whatever the case may be, one should consider conducting fish enzyme tests at the acclimation temperature of the fish, not at a standard temperature.

Acknowledgments

This research was funded, in part, by a research grant (WP-00369) from the Division of Water Supply and Pollution Control, U.S. Public Health Service, HEW.

BOUCK, G. R. 1966. Changes in blood and muscle composition of rock bass, (*Ambloplites rupestris*) as physiological criteria of stressful conditions. Ph.D. Dissertation. Michigan State Univ., East Lansing, Mich. 155 p.

BOUCK, G. R., AND R. C. BALL. 1965. Influence of a diurnal oxygen pulse on fish serum proteins. Trans. Am. Fish. Soc. 94: 363–370.

1966. Influence of capture methods on blood characteristics and mortality in the rainbow trout (*Salmo gairdneri*). Trans. Am. Fish. Soc. 95: 170–176.

1968. Comparative electrophoretic patterns of lactate dehydrogenase in three species of trout. J. Fish. Res. Board Can. 25: 1323–1331.

Burstone, M. S., and J. E. Folk. 1956. Histochemical demonstration of aminopeptidase. J. Histochem. Cytochem. 4: 217–226.

Cheeseman, E. M., A. M. Copping, and P. M. Prebble. 1967. Early changes in enzyme activity during the development and recovery from vitamin deficiency in the rat. Br. J. Nutr. 20: 413–420.

Delange, R. J., and E. L. Smith. 1971. Leucine amino peptidase and other N-terminal exopeptidases, p. 81–118. *In* P. O. Boyer [ed.] The enzymes. Vol. III. 3rd ed. Academic Press, Inc., New York, N.Y.

Felgenhauer, K., and G. G. Glenner. 1966a. Quantitation of tissue-bound renal aminopeptidase by a microdensitometric technique. J. Histochem. Cytochem. 14: 53–63.

1966b. The enzymatic hydrolysis of amino-acid-β-naphthylamides. II. Partial purification and properties of a particle-bound cobalt-activated rat kidney aminopeptidase. J. Histochem. Cytochem. 14: 401–413.

Giese, A. C. 1962. Cell physiology. W. B. Saunders Company, Philadelphia, Pa. 592 p.

Goldbarg, J. A., and A. M. Rutenburg. 1958. The colorimetric determination of leucine aminopeptidase in urine and serum of normal subjects and patients with cancer and other diseases. Cancer 11: 283–291.

Hess, B. 1963. Enzymes in blood plasma. Academic Press Inc., New York, N.Y. 166 p.

Hill, R. L., and E. L. Smith. 1956. Hydrolysis of amino acid amide derivatives of 2-aminofluorene, 4-aminobiphenyl and 4,4′-diaminobyphenyl by leucine aminopeptidase. Proc. Soc. Exp. Biol. Med. 92: 500–503.

Innerfield, I., R. Harvey, F. Luongo, and B. Lincoe. 1964. Urine peptidase activity following single and multiple oral doses of streptokinase. Proc. Soc. Exp. Biol. Med. 116: 573.

Johnson, M. J., and J. Berger. 1942. The enzymatic properties of peptidases, p. 69–92. *In* F. F. Nord and C. H. Werkman [ed.] Advances in enzymology. Vol. 2.

Law, G. R. J. 1967. Alkaline phosphatase and leucine aminopeptidase association in plasma of the chicken. Science 156: 1106–1107.

Lawrence, S. H. 1964. The zymogram in clinical medicine. Charles C. Thomas, Publisher, Springfield, Ill. 100 p.

Nachlas, M. M., B. Monis, D. Rosenblatt, and A. M. Seligman. 1960. Improvement in the histochemical localization of leucine aminopeptidase with a new substrate, L-leucyl-4-methoxy-2-naphthylamide. J. Biophys. Biochem. Cytol. 7: 261–270.

Patterson, E. K., S. Hsiao, and A. Keppel. 1963. Studies on dipeptidases and amino peptidases: I. Distinction between leucine aminopeptidase and enzymes which hydrolyze L-leucyl-β-naphthylamide. J. Biol. Chem. 238: 3611–3620.

Rabb, W. P. 1966. Renal enzyme excretion following anaphylactic shock. Nature (Lond.) 212: 953.

Smith, E. L. 1948. The peptidases of skeletal, heart, and uterine muscle. J. Biol. Chem. 173: 553–569.

Smith, E. L., and R. L. Hill. 1960. Leucine amino peptidase, p. 37–60. *In* P. O. Boyer, H. Lardy, and K. Myrback [eds.] The enzymes. Vol. 4, part A. 2nd ed. Academic Press, Inc., New York, N.Y.

Smith, E. L., J. T. Kaufman, and A. M. Rutenburg. 1965. The partial purification of an amino acid naphthylamidase from human liver. J. Biol. Chem. 240: 1718–1721.

Smith, E. L., and A. M. Rutenburg. 1963. Electrophoretic behavior of an aminopeptidase of human tissues and serum. Nature (Lond.) 197: 800–801.

1966. Starch gel electrophoresis of human tissue enzymes which hydroloyze l-leucyl-β-naphthylamide. Science (Wash., D.C.) 152: 1256–1257.

Smith, E. L., D. H. Spackman, and W. J. Polglase. 1952. The specificity of leucine aminopeptidase. III. Action on disastereoisomers. J. Biol. Chem. 199: 801–817.

Tarr, H. L. A. 1969. Contrasts between fish and warm blooded vertebrates in enzymes systems of intermediary metabolism, p. 155–176. *In* O. W. Neuhaus and J. E. Halver [ed.] Fish in research. Academic Press, Inc., New York, N.Y.

Wilkinson, J. H. 1965. Isoenzymes. J. B. Lippincott Company, Philadelphia, Pa. 158 p.

Uptake of Mercury by Freshwater Clams (Family Unionidae)

ANNETTE L. SMITH AND ROGER H. GREEN

Department of Zoology, University of Manitoba, Winnipeg, Man. R3T 2N2

AND ANDREW LUTZ

Department of the Environment, Fisheries and Marine Service, Freshwater Institute, Winnipeg, Man. R3T 2N6

SMITH, A. L., R. H. GREEN, AND A. LUTZ. 1975. Uptake of mercury by freshwater clams (family Unionidae). J. Fish. Res. Board Can. **32**: 1297–1303.

Mercury concentrations were measured in water, sediments, and three species of clams from lakes with and without reported mercury contamination. Elevated mercury levels in clams were associated with elevated mercury levels in water and sediments.

Uncontaminated clams were exposed to three mercury compounds at 1.0, 10, 50, and 100 μg Hg/liter for up to 3 wk in the laboratory. The clams concentrated the metal in the order methylmercuric chloride > phenylmercuric acetate > mercuric chloride. The rate of uptake of mercury increased with increasing mercury concentration in the water. In most cases, temperature had no effect on the rate of mercury uptake or elimination.

The distribution among organs depended on the compound to which the clams had been exposed. Only methylmercuric chloride was concentrated extensively in foot muscle. Transfer of methylmercuric chloride among organs apparently continued after exposure to the compound had ended.

SMITH, A. L., R. H. GREEN, AND A. LUTZ. 1975. Uptake of mercury by freshwater clams (family Unionidae). J. Fish. Res. Board Can. 32: 1297–1303.

Les auteurs ont mesuré les concentrations de mercure dans l'eau, les sédiments et trois espèces de coques provenant de lacs où on avait signalé ou non une contamination au mercure. Les hauts niveaux de mercure dans les coques sont liés aux niveaux élevés de mercure dans l'eau et les sédiments.

Des coques non contaminées furent exposées à trois composés de mercure à des concentrations de 1.0, 10, 50 et 100 μg Hg/litre durant des périodes allant jusqu'à 3 semaines au laboratoire. Les coques assimilent le mercure dans l'ordre chlorure méthylmercurique > acétate phénylmercurique > chlorure mercurique. Le taux d'assimilation du mercure augmente en fonction de la concentration du mercure dans l'eau. Dans la plupart des cas, la température n'affecte pas le taux d'assimilation ou d'élimination du mercure.

La répartition dans les organes dépend du composé auquel la coque a été exposée. Seul le chlorure méthylmercurique se concentre à un haut degré dans le muscle du pied. Le transfert du chlorure méthylmercurique d'un organe à l'autre semble se poursuivre après la fin de l'exposition au composé.

Received January 31, 1974
Accepted March 11, 1975

Reçu le 31 janvier 1974
Accepté le 11 mars 1975

BIVALVES are noted for their ability to concentrate trace metals (Pringle et al. 1968). Fimreite et al. (1971) have found mercury levels of 0.93–3.59 μg/g in both freshwater and marine clams collected near pulp mills and chlor-alkali factories.

Few studies have dealt with conditions influencing rates of uptake and release of mercury by molluscs. Hannerz (1968) reported concentration factors for mercury of up to 3570 times in gastropods exposed to inorganic and organic mercury compounds. Irukayama et al. (1962) found greater accumulation of alkyl mercury compounds than of inorganic or other organic mercury compounds by *Venus japonica*. Although some authors (Irukayama et al. 1962; Yoshida et al. 1967) have recorded varying mercury levels in different organs of bivalves depending upon the mercury compound to which the animals were exposed, no papers have dealt with differences in patterns of uptake and release by specific organs.

We have attempted to determine the effects of temperature, type of mercury compound, and mercury concentration on the rates of uptake and release of this metal by freshwater clams, and have considered variations in mercury levels and uptake–release patterns in several organs. Although clams can obtain mercury both from water and from food, only uptake from water is considered here.

Printed in Canada (J3301)
Imprimé au Canada (J3301)

Materials and Methods

SAMPLING PROCEDURES AND MERCURY ANALYSES

During the summers of 1970–72, *Anodonta grandis* were collected from several locations in Manitoba and northwestern Ontario, both with and without reported mercury contamination. In late summer 1971 and in 1972, sampling was concentrated in Minnedosa Lake, Man. (50°16′N, 99°48′W), and Clay Lake, Ont. (50°03′N, 93°30′W). Mercury levels in water, sediments, and the unionid clams *Lampsilis radiata* and *Lasmigona complanata*, in addition to *A. grandis* were determined.

In order to avoid loss of mercury, water samples were acidified in the field using 5 ml of concentrated H_2SO_4 for each 500 ml of water. Clams and sediments were frozen upon return to the laboratory.

Mercury analyses were performed on foot muscle, other individual organs, or whole clam. For whole clam determinations, soft tissues of individual clams were homogenized in a Waring blender, and samples of the homogenate analyzed. Frozen clams were dissected for analyses of separate organs. Mercury in clam tissues was determined by the wet digestion and flameless atomic absorption method of Armstrong and Uthe (1971).

Mercury was extracted from water samples by the dithizone method of Chau and Saitoh (1970). Sediments were prepared by Dow (1970) method. Aliquots of mercury extracts from water and sediments were used for mercury determination by flameless atomic absorption spectrophotometry (Armstrong and Uthe 1971).

For mercury uptake experiments, *A. grandis* from Mad Dog Lake, Ont., and Minnedosa Lake, Man., were acclimated to laboratory conditions for at least 2 wk and then placed in 30-liter aquaria containing dissolved mercury compounds. The water in each aquarium was changed daily and fresh mercury compound added, in order to assure that the mercury remained at the desired concentration. During mercury release experiments, the clams were held in constantly flowing clean water. Since the mercury concentration in the water might be altered by the formation and subsequent precipitation of mercury–food particle complexes, the clams were not fed during any of the experiments.

LABORATORY STUDIES OF MERCURY UPTAKE AND RELEASE

The rates of uptake and release of mercury were first studied by exposing the clams to mercuric chloride ($HgCl_2$), phenylmercuric acetate (PMA), and methylmercuric chloride (MMC), at 10, 50, and 100 μg Hg/liter at 10 and 20 C for 2 wk. The clams were then allowed to release mercury at these temperatures for an additional 2 wk. One clam per treatment was sampled at days 1, 4, 7, and 14 of the uptake and release periods. Background mercury determinations were performed on 18 clams prior to any exposure. Mercury analyses for this experiment were performed on foot muscle.

When subsequent experiments suggested that uptake and release of MMC by muscle tissue differs from uptake and release by other organs, a modified version of the first experiment was performed using homogenized whole clam for mercury analysis. Clams were exposed to MMC at 1.0 and 10.0 μg Hg/liter for 3 wk at 12 or 20 C and allowed to release mercury for 4 wk. Four clams (one per analytical sample) were used to determine background mercury levels, and individuals were sampled at uptake days 1, 4, 7, 14, and 21 and release days 2, 7, 14, 21, and 28.

From these two experiments we attempted to build a mathematical model to relate mercury concentrations in clams to the mercury concentration in the water from which the animals were collected.

The distribution of mercury among organs was studied using contaminated clams from Clay Lake. Initial mercury levels were measured in the mantle, gill, liver, and adductor muscle of five clams and the foot of seven clams. After the animals had been allowed to release mercury at 20 C for 8 wk, mercury concentrations in the same tissues of four additional clams were measured.

An experiment was designed to compare uptake and release of the three mercury compounds in three organs. After background mercury levels in the gills, foot, and liver of six replicate individuals were determined, clams were exposed to $HgCl_2$, PMA, and MMC at 50 μg Hg/liter for 4 days at 20 C, with two individuals per treatment sampled at days 1 and 4. The remaining clams were allowed to excrete mercury for 1 wk, with samples taken at 2, 4, and 7 days.

Mercury uptake data were analyzed by factorial analysis of variance and split-plot analysis of variance. Since release of Hg was assumed to follow an exponential curve, release data were treated by covariance analysis as linear regression of log (Hg) against time.

Results

Mercury concentrations were about 10 times higher in *A. grandis* from Clay Lake than from other waters (Table 1). Clams from the Winnipeg River system (Dorothy and Nutimik lakes) did not contain higher mercury levels than animals from the remaining locations, although mercury contamination has been reported in the Winnipeg River (Bligh 1971). Water apparently must be severely polluted before mercury concentrations in clams become elevated.

Clams, water, and wet sediments from Minnedosa Lake showed concentrations of mercury only 5–12% of those measured in Clay Lake (Table 2). There were highly significant ($P <$ 0.005) differences in mercury levels in whole clams between Minnedosa and Clay lakes. Differences among clam species were also highly significant, *A. grandis* concentrating less mercury than either *Lampsilis radiata* or *Lasmigona complanata*.

TABLE 1. Concentration of mercury in *Anodonta grandis* from various locations.

Location	Latitude	Longitude	Body part	Hg (μg/g)	No. specimens	SE
Red Rock L.	50°00′N	95°32′W	whole clam	<0.01	1	—
White L.	50°02′N	95°32′W	" "	<0.01	1	—
Betula L.	50°05′N	95°34′W	" "	<0.01	1	—
Mad Dog L.	49°36′N	93°48′W	foot	0.06	18	0.01
Minnedosa L.	50°16′N	99°48′W	foot	0.05	6	0.01
Minnedosa L.	"	"	gill	0.07	6	0.02
"	"	"	liver	0.06	6	<0.01
"	"	"	whole clam	0.01	6	<0.01
Nutimik L.	50°10′N	95°42′W	whole clam	0.01	1	—
Dorothy L.	50°11′N	95°45′W	" "	0.04	1	—
Dorothy L. narrows	50°11′N	95°45′W	liver	0.06	1	—
"	"	"	adductor	0.07	1	—
"	"	"	foot and visceral mass	0.07	1	—
Clay L.	50°03′N	93°30′W	mantle	0.47	5	0.03
"	"	"	gills	0.51	5	0.02
"	"	"	adductor	0.83	5	0.06
"	"	"	liver	0.78	5	0.07
"	"	"	foot	0.62	7	0.05
"	"	"	visceral mass	0.65	5	0.23
"	"	"	decalcified shell	0.08	4	0.03
"	"	"	whole clam	0.18	6	0.02

TABLE 2. Mercury concentrations of water, sediment, and clams from two lakes. Values are given as micrograms Hg per gram wet weight, except where noted. Values in parentheses are Hg levels expressed as a percentage of the mercury concentration of the same substance from Clay Lake.

Substance analyzed	Year	Lakes	
		Minnedosa	Clay
A. grandis (foot)	1971	0.05 (8.1%)	0.62
A. grandis (foot)	1972	—	0.40
A. grandis (homogenate)	1972	0.01 (5.6%)	0.18
L. radiata (foot)	1971	—	0.74
L. radiata (homogenate)	1972	0.03 (12.0%)	0.25
L. complanata (homogenate)	1972	0.03 (9.1%)	0.33
Water[a]	1972	0.01 (5.0%)	0.20
Sediment, wet	1972	0.01 (10.0%)	0.10
Sediment, dry	1972	0.04 (33.3%)	0.12

[a] Water (Hg) is given as μg Hg/liter.

UPTAKE AND RELEASE OF MERCURY

The mercury compound to which the clams were exposed was the most significant source of variation in uptake of mercury by clam foot muscle ($P < 0.01$). However, the concentration of mercury in the water was also significant ($P < 0.05$). Differences in temperature at which the experiment was run did not contribute significantly to differences in mercury uptake. There were no significant differences in slopes of the release curves among the treatments, and the pooled regression coefficient estimate of −0.037 per day was significantly different from zero. The test for differences in intercepts of the release curves, which is actually a test of mercury uptake, indicated ($P < 0.01$) that PMA is concentrated to a greater extent at 10 C than at 20 C. All other intercept tests were in agreement with the analyses of the uptake data.

Our model of uptake and release of mercury by clam foot muscle was similar to Ulfvarson's

(1962) model for mercury uptake and release in rats, except that his dosage constant was replaced by the uptake rate, which is a function of the mercury concentration in the water. The model with slight modifications fit the data, but the equation we obtained greatly underestimated the mercury levels in lakes to which the model was applied.

Both the length of exposure and the concentration significantly ($P < 0.01$) influenced uptake of MMC by whole clam, but temperature influence was not significant. Release rates were not significantly different from zero, nor did the slopes of the release curves differ with either temperature or concentration of mercury to which the clams had previously been exposed.

According to the Ulfvarson model, if the release rate of Hg were zero, then uptake would be described by a simple linear regression. This equation implies infinite capacity for uptake of mercury, which in practice would be modified if the number of binding sites for mercury in clam tissue approached saturation before the body burden of mercury proved fatal. For our data there was no significant deviation from a straight line regression. Thus, saturation of binding sites for mercury apparently was not approached during this experiment.

Since the release rate of mercury was negligible in this experiment, it was impossible to develop an equilibrium model of MMC uptake and release by whole clam.

DISTRIBUTION OF MERCURY AMONG ORGANS

Mercury was distributed unequally among the organs of *A. grandis* from Clay Lake. Significantly more mercury ($P < 0.01$) was concentrated per unit weight of adductor muscle, liver, and foot than of gill or mantle, while adductor also contained a significantly higher mercury concentration than did the visceral mass (Table 3).

TABLE 3. Distribution of mercury in the organs of *A. grandis* collected from Clay Lake. Means and standard errors of mercury concentrations are given as micrograms Hg per gram wet weight. The number of clams in each sample is given in parentheses.

Organ	Year clams collected	
	1971	1972
Mantle	0.47±0.01 (5)	—
Gill	0.51±0.01 (5)	—
Liver	0.78±0.02 (5)	0.47±0.07 (6)
Adductor	0.83±0.03 (5)	0.63±0.03 (6)
Foot	0.62±0.05 (7)	0.40±0.02 (14)
Visceral mass	0.65±0.08 (5)	—

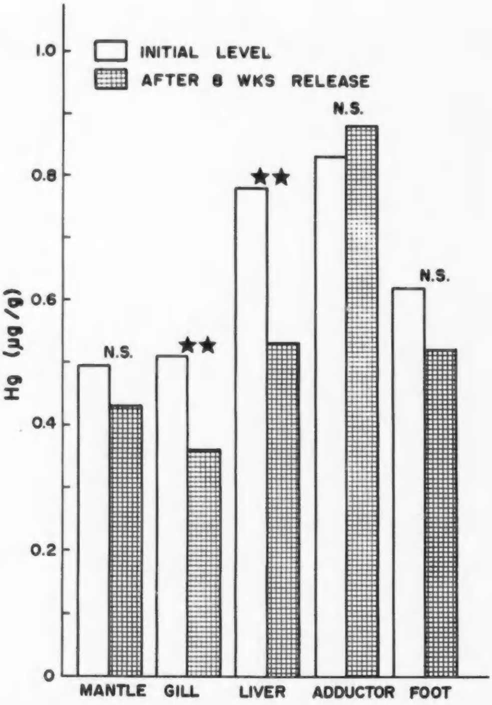


FIG. 1. Change in mean mercury concentration in several tissues of *Anodonta grandis* from Clay Lake after an 8-wk period in uncontaminated water.

In contaminated clams allowed to release mercury in the laboratory, elimination of the metal over the 8-wk period varied among tissues (Fig. 1). Although the mercury concentration of gill and liver decreased significantly ($P < 0.01$), change in mercury concentration of mantle, adductor muscle, and foot was not statistically significant.

The patterns of uptake and release of mercury by various tissues in the laboratory suggested a complex pattern of mercury transfer (Fig. 2). Among-organ differences in mercury uptake were highly significant ($P < 0.01$), with liver and gill concentrating more mercury per unit weight than foot muscle. During the 4-day exposure, the form in which the mercury was administered ($HgCl_2$, PMA, or MMC) did not significantly influence uptake.

The decrease in mercury concentration after transfer to clean water was highly dependent ($P < 0.01$) upon the compound to which the animals had been exposed, with the order of retention of

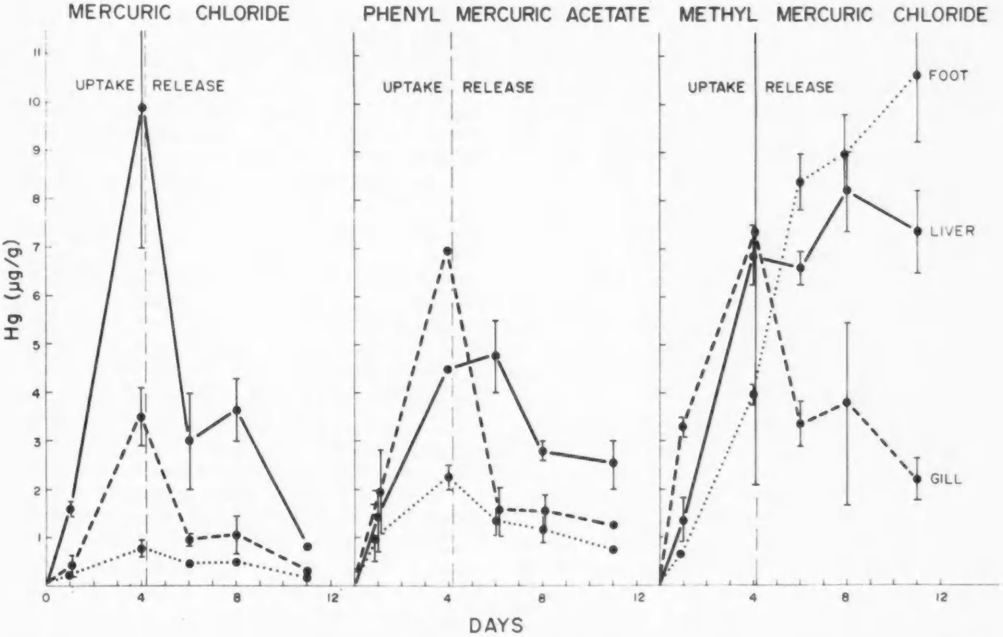


FIG. 2. Uptake and release of three mercury compounds by *A. grandis* gill, foot, and liver at 20 C. Mercury concentration in the water during the uptake portion of the experiment was 50 μg/liter. Bars represent standard errors.

compounds being MMC>PMA>$HgCl_2$. Individual organs also varied in their release of mercury. In general, gill lost the most mercury per unit weight and liver the least. A strong interaction ($P < 0.01$) between mercury compound and organ was present. Figure 2 suggests that this interaction is due to the rapid loss of $HgCl_2$ from the liver while MMC is retained by that organ, and to the increase in the concentration of MMC in foot muscle after termination of exposure.

The mercury concentration in clams at the end of the uptake experiment was significantly higher than that in clams after transfer to clean water for 2 days; but there was no significant change in mercury levels between day 2 and the end of the release experiment. Apparently there is a change in the slope of the release curve, with rapid loss of mercury during the first 2 days after exposure ends, followed by a period of much slower release or no release of the remaining mercury.

Discussion

UPTAKE AND RELEASE OF MERCURY

The concentration of mercury in clam tissue depends on the compound to which the animals have been exposed but two experiments suggest conflicting reasons for compound-dependent differences. The study involving only foot muscle suggests that each compound is taken up at a different rate, but that there is no significant difference in the rates at which different compounds are released. However, the experiment including several organs implies that there is no difference in the instantaneous rate of uptake but that long-term differences in the tissue concentrations of mercury are dependent upon the degree of retention of each compound.

The second of these conclusions seems the more reasonable since several researchers have found that in mammals methyl mercury is excreted more slowly than PMA (Gage 1964) or inorganic mercury (Berlin and Ullberg 1963; Takahashi and Hirayama 1971). The compound-dependent differences in mercury retention in different organs apparently are due to a rapid (48 h or less) loss of unbound mercury, followed by slower release of the remaining metal. Methyl mercury binds more tightly to tissues than inorganic forms (Brown and Kulkarni 1967), which accounts for the greater retention of that compound.

Compound-dependent differences in the release of unbound mercury from foot muscle may not have been detected because release was not measured until the clams had been in clean water for 24 h. Further experiments of several months' duration might demonstrate differences in the long-term release rates of the bound mercury compounds.

Pringle et al. (1968) have reported that temperature is closely related to uptake rate and ultimate concentration of a given metal. However, the results of our experiments do not support this observation. No significant differences in uptake rates or concentrations attained were observed at different temperatures, except that PMA was concentrated in foot muscle to a greater extent at 10 C than at 20 C.

Lack of temperature dependence of uptake rates suggests that uptake is by diffusion followed by the formation of stable complexes within the animals, a process considered likely by Craig (1967). The other possible mechanism of concentration, active uptake, is linked with the metabolic activities of the cells and has a higher temperature coefficient than simple diffusion (Pringle et al. 1968). Accumulation of mercury apparently depends on the strength and degree of binding, which is consistent with the formation of stable complexes.

The higher uptake of PMA by foot muscle at 10 C was unexpected and is difficult to explain. It may represent organ-specific temperature dependence. Vernberg and O'Hara (1972) have shown that the gills of *Uca pugilator* concentrate mercury to a greater extent at low temperature than at high temperature because the animal is better able to transfer mercury from the gills at higher temperature. Although no temperature-dependent differences in the release of bound PMA were observed, the higher concentration of mercury in foot muscle at 10 C may represent diminished ability to transport the unbound mercury compound from that organ.

Variations in the release rates at different temperatures were expected and have been reported in fish (Jarvenpaa et al. 1970). We could not demonstrate these differences, but if the half-life of bound mercury in clams is on the order of several hundred days, as the MMC data suggest, temperature-dependent differences would be difficult to detect in experiments of 14–28 days' duration.

DISTRIBUTION OF MERCURY AMONG ORGANS

High initial accumulation of mercury in the gills of clams exposed to mercury in the laboratory suggests that some uptake occurs across these organs. Diffusion of mercury from the water across the gills has been reported in several aquatic organisms (Corner 1959; Jernelov and Lann 1971; Jones et al. 1972). Korringa (1952) found that positive polyvalent ions adhere to the mucous feeding sheets of oysters. Since the mucous sheets of *A. grandis* pass across the gills, some of the mercury concentration measured in the gills might be attributed to contaminated mucus.

Methylated mercury is metabolized by the liver of rats (Takahashi and Hirayama 1971). The sustained high level of MMC in the liver of *A. grandis* suggests similar importance of clam liver in the metabolism of MMC.

Only small amounts of $HgCl_2$ and PMA were accumulated in foot muscle during the 1-wk exposure, and these apparently were excreted in clean water. However, the mercury concentration in the foot muscles of animals exposed to MMC continued to increase after exposure had ended. A similar situation is suggested by Jernelov and Lann (1971), who report that methyl mercury, but not inorganic mercury, is slowly eliminated from liver and subsequently accumulates in muscle. They explain that any change in the relation between accumulation and excretion is observed in the liver before it is seen in the muscle due to the higher metabolic rate of liver. Apparently there is a complicated system of transfer of methylated mercury in and out of the organism. However, in our study it is also possible that, because the clams were not fed, loss of weight contributed to the observed increase in mercury concentration.

Acknowledgments

We would like to express our appreciation to F. A. J. Armstrong for advice, and for critically reviewing this manuscript in an earlier draft. This research was supported by a grant from the Department of the Environment.

ARMSTRONG, F. A. J., AND J. F. UTHE. 1971. Semi-automated determination of mercury in animal tissue. At. Absorpt. Newsl. 10: 101–103.

BERLIN, M., AND S. ULLBERG. 1963. Accumulation and retention of mercury in the mouse. III. An autoradiographic comparison of methylmercuric dicyandiamide with inorganic mercury. Arch. Environ. Health 6: 610–616.

BLIGH, E. G. 1971. Mercury in Canadian fish. Pacific Fisheries Technologists Conference, Victoria, B.C. March 22–24, 1971.

BROWN, J. R., AND M. V. KULKARNI. 1967. A review of the toxicity and metabolism of mercury and its compounds. Med. Serv. J. Can. 23: 786–808.

CHAU, Y. K., AND H. SAITOH. 1970. Determination of submicrogram quantities of mercury in lake waters. Environ. Sci. Technol. 4: 839–841.

CORNER, E. D. S. 1959. The poisoning of *Maia squinado* (Herbst) by certain compounds of mercury. Biochem. Pharmacol. 2: 121–132.

CRAIG, S. 1967. Toxic ions in bivalves. J. Am. Osteopath. Assoc. 66: 1000–1002.

DOW CHEMICAL COMPANY. 1970. Dow–Sarnia Analytical Laboratory Report Method. CAS-AM-70. 10.

FIMREITE, N., W. N. HOLSWORTH, J. A. KEITH, P. A. PEARCE, AND I. M. GRUCHY. 1971. Mercury in fish and fish-eating birds near sites of industrial contamination in Canada. Can. Field-Nat. 85: 211–220.

GAGE, J. C. 1964. Distribution and excretion of methyl and phenyl mercury salts. Brit. J. Ind. Med. 21: 197–202.

HANNERZ, L. 1968. Experimental investigations on the accumulation of mercury in water organisms. Rep. Inst. Freshwater Res. Drottningholm 48: 120–176.

IRUKAYAMA, K., M. FUJIKI, F. KAI, AND T. KONDO. 1962. Studies on the origin and causative agent of Minamata disease. II. Comparison of the mercury compound in the shellfish from Minamata Bay with mercury compounds experimentally accumulated in control shellfish. Kumamoto Med. J. 15: 1–12.

JARVENPAA, T., M. TILLANDER, AND J. K. MIETTINEN. 1970. Methylmercury: half-time of elimination in flounder, pike, and eel. Suom. Kemistil. B. 43: 439–442.

JERNELOV, A., AND H. LANN. 1971. Mercury accumulation in food chains. Oikos 22: 403–406.

JONES, A. M., Y. JONES, AND W. D. P. STEWART. 1972. Mercury in marine organisms of the Tay region. Nature 238: 164–165.

KORRINGA, P. 1952. Recent advances in oyster biology. Q. Rev. Biol. 27: 266–308.

PRINGLE, B. H., D. E. HISSONG, E. L. KATZ, AND S. T. MULAWKA. 1968. Trace metal accumulation by estuarine mollusks. Am. Soc. Civil Eng. Proc. J. Sanitary Eng. Div. 94(SA3), Paper 5970: 455–475.

TAKAHASHI, H., AND K. HIRAYAMA. 1971. Accelerated elimination of methyl mercury from animals. Nature 232: 201–202.

ULFVARSON, U. 1962. Distribution and excretion of some mercury compounds after long term exposure. Int. Arch. Gewerbepath. Gewerbehyg. 19: 412–422.

VERNBERG, W. B., AND J. O'HARA. 1972. Temperature-salinity stress and mercury uptake in the fiddler crab, *Uca pugilator*. J. Fish. Res. Board Canada 29: 1491–1494.

YOSHIDA, T., T. KAWABATA, AND Y. MATSUE. 1967. Transference mechanism of mercury in marine environments. Tokyo Univ. Fish. 53: 73–84.

Spatial Model for an Exploited Shellfish Population, and its Application to the Georges Bank Scallop Fishery

J. F. CADDY

Department of the Environment, Fisheries and Marine Service, Biological Station, St. Andrews, N.B. E0G 2X0

CADDY, J. F. 1975. Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery. J. Fish. Res. Board Can. 32: 1305–1328.

Existing fisheries models employ the "unit stock" concept that makes no explicit allowance for spatial distribution of biomass and effort over a fishing ground. The utility of the unit stock concept rests largely upon the "dynamic pool" assumption. However, this is both invalid for sedentary species, and difficult to apply when information on spatial distribution by statistical subunits is available, as for the Georges Bank (lat. 42°N, long. 67°W) scallop population. By reference to the Georges Bank scallop fishery, more realistic general assumptions for a spatial model of shellfish populations are:

a) Recruitment occurs in patches of random size and location with the constraint that local biomass does not exceed the virgin biomass of each unit area.

b) The fraction of effort expended within each statistical area of a fishing ground is either determined by available local biomass alone (proportional effort allocation) or in combination with "traditional fishing practice."

Therefore, a spatial model (YRAREA) simulating nonrandom recruitment and harvesting of sedentary organisms is postulated and applied to Georges Bank scallop stocks. Some of the general predictions of this model differ significantly from those employing the unit stock concept, as follows:

1) Under proportional effort allocation, overall yield declines more sharply with increasing effort subsequent to maximum sustained yield (MSY) than under dynamic pool assumptions. 2) Peak mortality and the apparent point of full recruitment on the catch curve occur progressively earlier in life (even at partially recruited ages) with increased effort or degree of clumping of the population, and subsequently declines with age, except where "fully recruited" ages coincide spatially with the "target" age-group making up the largest biomass component. This may be of general relevance to fisheries under intensive exploitation with sophisticated methods of navigation and fish finding; peak mortality may occur earlier in life than predicted from the gear selection ogive, if year-classes are independently distributed and there is no size limit regulation. 3) Variance in biomass/unit area is predicted to fall with age.

For the Georges Bank scallop population, the model described herein predicts that a substantial increase in yield would result from diversion of effort from the Northern Edge to less heavily fished areas of the bank.

CADDY, J. F. 1975. Spatial model for exploited shellfish population, and its application to the Georges Bank scallop fishery. J. Fish. Res. Board Can. 32: 1305–1328.

Les modèles de pêcheries actuels utilisent le concept d'« unité de stock », qui ne tient pas explicitement compte de la distribution spatiale de la biomasse et de l'effort sur un lieu de pêche donné. Le concept d'unité de stock repose en grande partie sur l'hypothèse du « pool dynamique ». Cependant, cette hypothèse ne tient pas dans le cas d'espèces sédentaires et est de plus difficile d'application quand on connait la distribution spatiale par sous-unités statistiques, comme c'est le cas de la population de pétoncles du banc Georges (42° lat. N, 67° long. W).

En ce qui concerne la pêcherie de pétoncles du banc Georges, des hypothèses générales plus réalistes sur lesquelles fonder un modèle spatial de populations de pétoncles sont les suivantes:

a) Le recrutement se produit par groupes dont la répartition et la grandeur sont laissées au hasard, avec la restriction que la biomasse locale ne dépasse pas la biomasse vierge de chaque unité de superficie.

b) La fraction de l'effort dans chaque région statistique d'un lieu de pêche est déterminée soit par la biomasse locale disponible seule (allocation proportionnelle de l'effort), soit en association avec la « pratique de pêche traditionnelle ».

Nous construisons donc un modèle spatial (YRAREA) simulant un recrutement et une récolte intentionnels d'organismes sédentaires et l'appliquons aux populations de pétoncles du

Printed in Canada (J3397)
Imprimé au Canada (J3397)

banc Georges. Quelques-unes des prédictions générales de ce modèle diffèrent de façon significative de celles qui sont fondées sur le concept d'unité de stock, comme suit:

1) Si l'on utilise une allocation proportionnelle de l'effort, le rendement global diminue plus brusquement à mesure qu'augmente l'effort au-delà du rendement maximum soutenu que lorsqu'on se sert d'hypothèses de pool dynamique. 2) Les mortalités de pointe et le point apparent de plein recrutement sur la courbe des prises se produisent de plus en plus tôt dans la vie (même aux âges de recrutement partiel) à mesure que l'effort ou le degré de groupement en masse compacte de la population augmentent, pour diminuer par la suite avec l'âge, sauf dans le cas où les âges pleinement recrutés coïcident dans l'espace avec le groupe d'âge « cible » qui constitue la plus grande composante de la biomasse. Ceci peut avoir une applicabilité générale pour les pêcheries soumises à une exploitation intensive par des méthodes raffinées de navigation et de détection du poisson; les mortalités de pointe peuvent se produire à un âge moins avancé que celui prédit par l'ogive de sélection des engins de pêche, si les classes d'âge sont réparties indépendamment les unes des autres et s'il n'y a pas de règlementation quant à la taille limite. 3) Nous prédisons que la variance dans la biomasse/unité de superficie baissera avec l'âge.

Le modèle décrit dans cet article prédit que, dans le cas de la population de pétoncles du banc Georges, une diversion de l'effort depuis l'accore nord vers des régions du banc où la pêche est moins intensive contribuerait à augmenter de façon substantielle le rendement.

Received April 11, 1974
Accepted April 7, 1975

Reçu le 11 avril 1974
Accepté le 7 avril 1975

FEW models for exploited animal populations have gained wide acceptance in fishery management circles; these have been classified by Schaeffer (1968) into dynamic pool models (e.g. Ricker 1940, 1944; Beverton and Holt 1957), and logistic models (e.g. Schaeffer 1954, 1957; Pella and Tomlinson 1969). Both approaches deal with a unit stock, defined as a closed, self-sustaining unit of population, in which fishing mortality (F) is proportional to fishing effort (*f*). However, only if the area exploited and the relative distribution of stock and effort are constant does catchability (*q*) in the equation $F = q.f.$ remain constant from year to year (Paloheimo and Dickie 1964). Thus, the Beverton and Holt (1957) model requires that relative distribution of fish and gear should not be determined primarily by their ability to perceive one another. Evidently, only in a theoretical situation, namely a uniform distribution of effort over the whole stock area, can there be equal probabilities of capture for all individuals, for both immotile and motile organisms.

Because a stock is often contagiously distributed (e.g. Taylor 1953), an entire population is not equally vulnerable to fishing effort within any short time interval. To reconcile with the above theoretical requirements the heterogeneous distribution of stock and effort that prevails in all fisheries to at least some extent, active dispersal is invoked to spread local effects of past effort uniformly across the unit stock, so that locally depleted areas are replenished by immigration (Ricker 1944). This is evidently impossible for sedentary animals showing a contagious distribution, and hence the relation between effort and fishing mortality departs from simple proportionality. It seems intuitively obvious that areas of seafloor occupied by dominant year-classes (often at high density) will then suffer heavy mortality, while low density areas may suffer little or no fishing mortality. If position of peak recruitment varies annually, a spatial "mosaic" of annual mortality rates arises, which incidentally compounds the problem of estimating population parameters from catch samples.

The approach of Baranov (1918), and later elaborations (Treschev 1973), express the relation between effort and mortality in terms of area or volume swept by the gear over a uniformly distributed population. A precondition for application of these "elemental" models is that stock and effort be distributed randomly if there is to be equal probability of capture of all individuals. Because this precondition is rarely satisfied, yield must be summed over subareas within which the assumption of random distribution is more realistic. This approach may still underestimate mortality, if distribution within unit areas is contagious (Beverton and Holt 1956), but may be compensated by adjustment of the elemental catchability coefficient *q*′, if an independent mortality estimate is available for the whole stock.

The consequences of departures from uniform effort distribution were noted by Baranov (1918) who pointed out that age composition in commercial samples will not represent the whole population if fishermen concentrate on larger schools made up of stronger year-classes. Paloheimo and Dickie (1964) recognized that fishermen take advantage of stock contagion even without accurate information on patch location and extent by remaining in areas where catches are high, and moving randomly following a poor catch. The latter authors used spatial components of stock distribution and fleet searching efficiency in their harvesting model but were obliged to make a number of restricting assumptions to obtain an analytical solution for the relation between schooling behavior and catch per unit effort; namely uniform school size and intraschool density, and low density of schools with no overlapping.

For many species, especially scallops (Dickie 1955), extremely irregular recruitment is the norm, and Thorson (1946) pointed out that such fluctuations are especially evident in invertebrates with long planktonic lives and planktotrophic larvae (as in many commercially important molluscs and crustacea). The need for specific larval settlement surfaces in many benthic invertebrates means that successful settlement depends on the coincidence of a larva ready to metamorphose and a suitable settlement surface; a configuration dependent on prevailing hydrographic conditions. Good recruitment in shellfish often follows catastrophic mortality of the adult population due to unfavorable environmental conditions. Winter kills of mussel, *Mytilus edulis* (Savage 1956) and cockle, *Cerastoderma edule* (Kristensen 1959) populations are often followed by heavy spatfalls. The high fecundity of many invertebrates allows this, but the critical factor seems to be the "available space" vacated due to adult mortality. In a two-dimensional universe, intraspecific competition for available space is likely to be more acute than for many fish species.

Although larval stages of many sessile epifaunal organisms are attracted to adult populations at metamorphosis, this may result in poor survival, because in competition for limited space and food, adult forms are more resistant to adverse environmental effects and food shortage by virtue of their lower metabolic rate. Hancock (1970) found a significant inverse correlation between number of recruits and total stock size (including immature postrecruits) in cockle populations, and Davis (1923) noted for populations of the clam, *Spisula subtruncata*, that consecutive age-groups do not occur on the same ground, suggesting exclusion of juveniles from dense adult populations.

The concept of a maximum population size basic to the Schaeffer (1957, 1968) and Generalized Production (Pella and Tomlinson 1969) models, (and implicit in the Ricker spawner–recruit model) implies for populations below the maximum size, the concept of "available space" for new recruitment. Because data on prerecruits are usually lacking, in the present model the recruitment constraint is applied at the time of first availability to the gear rather than at metamorphosis from the plankton. For an age-structured population, limiting population size is best expressed in terms of biomass. "Available space" can then be defined as the difference between some hypothetical maximum biomass and the actual population biomass. Such constraints on recruitment may operate locally without necessarily operating for the stock as a whole, and in this approach, total annual recruitment to the population (N_T) is held constant, but local constraints on recruitment are imposed by some hypothetical maximum density.

Temporal and Spatial Variations of Catch and Effort in Georges Bank Scallop Fishery

ANNUAL CATCH AND EFFORT STATISTICS

Catch and nominal effort (days fished) data for U.S. and Canada have been analyzed by 10′ statistical unit areas from 1957 to 1968 inclusive during which period catches were recorded from a total of 166 unit areas (Table 1). As noted by Bourne (1964) and J. A. Posgay (personal communication) effort and catch distribution is far from uniform. Three regions, the Northern Edge, Northeast Peak, and Southwest Channel, provide most of the catch—83% of landings in 1944–61 came from 38% of the area of the bank within the 50-fath isobath. Data on Canadian catch and effort distribution over the bank came from log records completed by 70–75% of the fleet. Effort and catch were recorded separately by 10′ unit areas (Tables 1A, B) and the resulting distributions used to prorate unallocated catches obtained from landing slips. Comparable U.S. data are obtained by port interview. The earlier U.S. landings and effort data (Posgay 1953) identify U.S. catch from Georges Bank with landings at New Bedford, and since Canadian effort data are not available for 1951–56, effort in this period is estimated in U.S. units:

$$\begin{array}{c}\text{Days fished}\\ \text{(U.S. units)}\end{array} = \frac{\text{Canadian catch}}{\text{U.S. catch per unit effort}}$$

and added to the U.S. effort.

Gear dimensions have remained relatively constant for the U.S. fleet: Royce (1946) and Posgay (1957) both considered two 11-ft (3.35-m) wide dredges as standard. Engine horse power and vessel size have increased, but the shucking operation is the major limitation on fishing power so that effects of mechanization may be less obvious than in many other fisheries. Larger vessels and crew and two 12–13-ft (3.7–3.9-m) dredges are standard for the Canadian fleet, and a rough estimate of relative fishing power based on regression through the origin of mean catch per

TABLE 1.

A) Mean annual catch (U.S. and Canada) in metric tons of meats per 10′ unit area of lat. and long. (C_{ij}) for 1957–68 inclusive

					69°						68°						67°						66°	
													9	45	230	494	794	520	449	209	133	35	5	
											10	37	21	46	194	193	114	66	555	266	225	290	69	42°
									35	12	13	13	4	7	51	23	23	11	30	57	121	263	189	
	1	2	1					9	57	5	3	1	3		1	2	7	10	9	49	191	264	99	
		5	31	1			20	44	33	9	7			6	5		7	13	60	264	230	69		
	5	4	19	19	11	46	64	42	7	6				2		6	24	14	24	71	70			
1			22	120	66	75	219	90	10	5	4	4	17	19	37	23	29	35	35	42	7			41°
6		3	16	74	150	94	20	9	15	8	9	18	72	370	197	202	116	15	5					
4			6	26	63	25	9	9	15	71	82	108	196	124	32	9								
9		3		6	12	20	20	33	32	12	4	4	9	11										
				15		7	3	4																

B) Mean nominal effort (U.S. and Canada) in days fished per 10′ unit area of lat. and long. (f_{ij}) for 1959–68 inclusive.

					69°						68°						67°						66°	
													9	43	218	484	741	515	441	212	139	37	7	
											10	40	22	46	199	209	118	72	582	285	234	305	74	42°
									33	27	13	18	4	5	57	24	25	11	32	65	150	292	205	
	2	5	3					9	58	4	4	2	4		1	3	7	8	11	54	199	266	106	
		5	32	2			21	49	36	10	7			7	5		6	14	66	291	228	72		
	6	6	20	20	10	45	63	45	8	6				3		6	29	16	27	80	72			
2			22	119	63	77	238	95	10	6	5	4	17	21	39	26	37	43	41	49	7			41°
8		2	16	77	171	104	25	11	19	6	9	21	79	357	199	203	120	15	6					
7			7	27	66	28	10	10	18	75	85	114	168	105	30	10								
10		4		7	15	23	24	37	39	14	4	4	17	10										
				17		10	4	5																

C) Estimated virgin biomass per 10′ unit area of lat. and long. ($B_{\max_{ij}}$) in metric tons.

					69°						68°						67°						66°	
													137	568	2263	6727	7297	7297	5851	2034	1206	480	357	
											140	497	309	571	1861	1876	1035	652	8265	2871	2259	3208	675	42°
									512	168	185	195	55	103	562	339	337	155	439	582	1100	2860	1823	
	13	33	20					137	614	70	50	20	40		13	33	108	146	135	554	1830	2771	904	
		70	454	20			288	525	458	126	103			90	66		100	185	609	2873	2291	681		
	80	53	282	275	157	577	659	527	108	82				30		92	356	202	346	689	698			
20			317	1085	686	729	2212	828	150	76	64	61	243	280	493	339	402	452	464	496	98			41°
95		42	236	724	1394	858	296	137	220	113	132	269	702	4381	1888	1949	1045	220	74					
63			93	386	634	365	127	130	226	703	779	977	1806	1127	469	138								
137		50		89	181	290	294	456	429	171	61	56	280	154										
				219		108	51	66																

TABLE 2. Catch statistics for Canadian and U.S. sea scallop fleets fishing Georges Bank, 1944–71 inclusive.

Year	Landings of scallop meats (metric tons)			Effort in days on the grounds			CPUE (MT/day)
	U.S.	Canada	Total	U.S.	Canada	Total	
						(Can. units)	
1944	1,814	—	1,814	2,223	—	2,039	.890
1945	1,769	—	1,769	2,391	—	2,194	.806
1946	4,036	—	4,036	4,934	—	4,527	.892
1947	4,853	—	4,853	6,434	—	5,903	.822
1948	4,580	—	4,580	7,613	—	6,984	.656
1949	5,306	—	5,306	8,428	—	7,732	.686
1950	5,442	—	5,442	7,349	—	6,742	.807
1951	5,714	91	5,805	7,626	(123)	7,119	.815
1952	5,488	91	5,579	7,742	(128)	7,231	.772
1953	7,392	136	7,528	10,031	(185)	9,388	.802
1954	7,029	91	7,120	9,343	(121)	8,693	.819
1955	8,299	136	8,435	11,619	(190)	10,850	.777
1956	7,937	317	8,254	12,246	(490)	11,725	.704
1957	7,846	771	8,617	10,500	1,197	10,830	.796
1958	6,531	1,179	7,710	8,775	1,598	9,648	.799
1959	8,481	1,950	10,431	8,556	2,098	9,948	1.049
1960	9,932	3,401	13,333	8,039	2,601	9,976	1.337
1961	10,703	4,580	15,283	8,671	3,147	11,102	1.377
1962	9,932	5,669	15,601	8,959	4,642	12,861	1.213
1963	7,982	5,941	13,923	7,718	5,905	12,986	1.072
1964	6,122	5,986	12,108	6,662	6,723	12,835	.943
1965	1,497	4,580	6,077	2,156	5,749	7,727	.786
1966	998	4,853	5,851	1,001	5,524	6,442	.908
1967	1,315	5,034	6,349	1,870	6,785	8,501	.747
1968	1,179	4,807	5,986	1,938	6,972	8,750	.684
1969	1,769	4,354	6,123	2,800	6,684	9,253	.662
1970	1,497	4,036	5,533	2,706	7,615	10,098	.548
1971	1,406	3,946	5,352	2,577	7,688	10,052	.532

day for the two national fleets for the period 1961–71 gives:

$$(c/f)_{\text{CAN.}} = 1.09\,(c/f)_{\text{U.S.}}$$

suggesting that fishing power is almost in the ratio of standard dredge widths for the two countries. This factor was used to convert U.S. effort data to Canadian units before combining to give effort in days fished by the two national fleets (Table 2).

RELATION BETWEEN CATCH AND FISHING EFFORT

Combined U.S. and Canadian statistics (Table 2) suggest that events before and after 1959 should be examined separately. Catch increased almost linearly with effort up to 5000 MT by the late 1950s and the relatively small variance in catch at a given effort level indicates that the 1944–58 data approximate well to some equilibrium condition (Fig. 1). From 1959–64, CPUE was well above the "equilibrium level" of the preceding years and total effort increased to a maximum of 13,000 days in 1963, while catch per unit effort continued the steady decline begun in 1962 and did not level off until 1966. The drop in effort and return to the "equilibrium line" in 1966–67 coincides with the decline in U.S. effort on Georges Bank and temporary diversion of Canadian effort to ICNAF area 6. Since 1965, catches have remained steady at around 6000 MT, and declined slowly with increasing effort, suggesting that a new equilibrium may have been reached at a lower biomass level than before 1959. The most obvious factor accounting for this decline is the reduction in age at first capture from age 5 to age 3–4 described by Caddy (1971a) and Brown et al. (1972).

DISTRIBUTION OF SCALLOPS AND FISHING EFFORT ACROSS THE BANK

Heavier and more regular recruitment and higher fishing intensity on the Northern Edge results in an overall decrease in average size and increase in abundance from south to north on

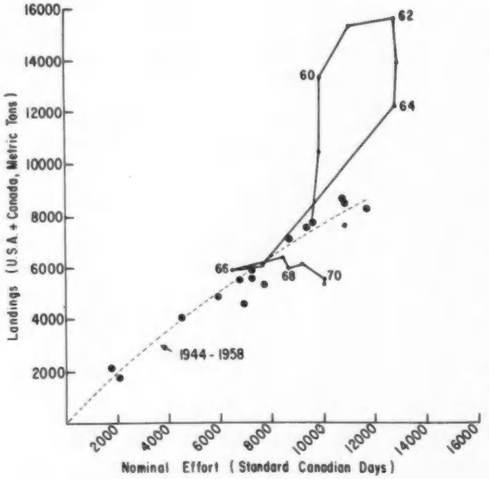


FIG. 1. Historical catch and effort relation for the Georges Bank fishery. A line is fitted by eye through the data points for 1944–58 inclusive. Subsequent years are separately identified.

the bank. This cannot be accounted for by differential growth rates, or by migration (Posgay 1963).

The distribution pattern of a patch of new recruits on the Northern Edge was investigated by underwater photography in 1970 and 1971, and revealed peak densities of four to five new recruits (age 3 and 4)/m^2 that fell off with distance from the center of the patch. Large scallops were relatively sparse ($<0.5/m^2$) and uniform throughout the area (Fig. 2a). A significant proportion of Canadian effort in 1970 concentrated in this area (Fig. 3), and both commercial (Fig. 4a) and research vessel catches (Fig. 4b) for the year reflected an inverse relation between both meat and shell size and total size of the catch, whether per trip, or per tow. A photo survey of the same area in 1971 (Fig. 2b) revealed that densities of all sizes were low throughout the area, and a local fishing mortality rate of $F = 1.18$ was estimated (Caddy 1972).

Evidently the commercial fleet is very successful at searching out and depleting areas of high biomass, and at low stock density these are inevitably areas of new recruitment. It is tentatively concluded that under these circumstances the fishing mortality rate for new recruits will exceed that for older more dispersed individuals.

Description of the Model

The model considers a fishing ground and its sedentary population of recruits as a matrix of unit areas with no intermigration. As such it applies to most shellfish species. A program (YRAREA)[1] was developed with L. E. Gales of the Norfish group, University of Washington for a CDC 6400 computer to describe the effects of aimed fishing on a clumped population of sedentary organisms (Fig. 5). A specified number of recruits are added to the population each year, patch shape being described by a bivariate normal distribution in which local densities are constrained by a maximum biomass per unit area, and patch size and position determined by uniform random numbers. Total fishing effort is allocated to the matrix of unit areas in proportion to the potential catch per unit effort realizable from each. Catch and residual population are calculated using age-specific fishing, and constant natural mortality rates and summed over age and area to give annual totals for the whole population. Variances of area-specific catch, effort, and catch per unit effort are calculated to give concentration indices I_g and I_r.

The simulation is run for a life span (L years) for each parameter set, and in the Lth year, area-specific values are printed out for fishing effort, catch, mean size, and residual biomass before reinitializing and running with different values for the input parameters. The only stochastic elements introduced are in distributing the recruits and even this may be limited by carrying capacity of a unit area, and existing postrecruit biomass. All other rates are deterministic, and no allowance is made for possible density dependent effects on growth and natural mortality.

LARGE-SCALE DISTRIBUTION PATTERN

A "fishing ground" is an area where there is a high probability of encountering exploitable densities of organisms and is enclosed by a matrix X* (Fig. 6) consisting of S × T unit areas (S and T are odd numbers) each $s \times t = A$ km^2 in area; unit area a_{yz} being the central unit area of the matrix:

$$X^* = \begin{bmatrix} a_{11} & & a_{1T} \\ & a_{yz} & \\ a_{S1} & & a_{ST} \end{bmatrix}$$

One or more exploitable concentrations ("beds")

---

[1] A listing and description of program **YRAREA** is available from the author.

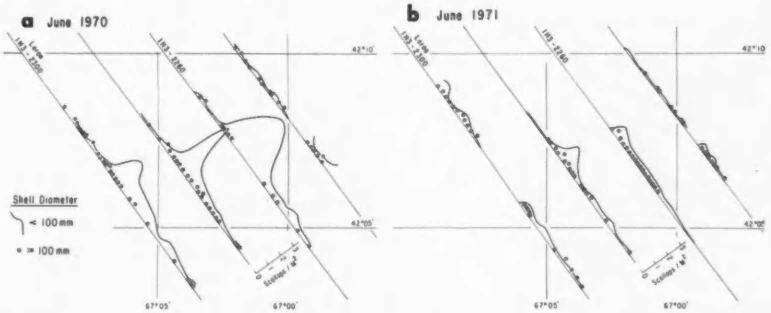


FIG. 2. Two surveys by underwater photography of an area of high density recruitment on the Northern Edge of Georges Bank before and after intensive commercial exploitation. Tows were made with a dredge-mounted camera along Loran 1H3 lines, and estimates of population density of two size-groups averaged over 2-min periods for 1.30 m² bottom photos.

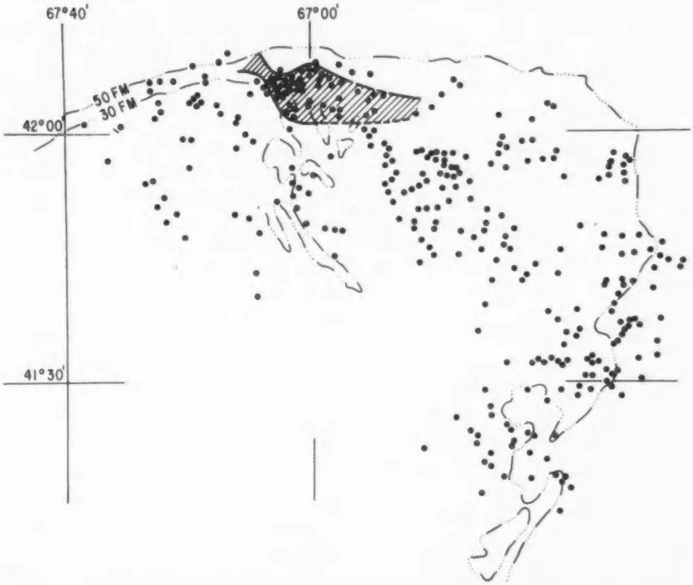


FIG. 3. Positions fished by a sample fleet of 18 Canadian boats during the first half of 1970 (extent of high density recruitment area shown in Fig. 2a shaded).

are distributed randomly over the matrix; beds of the same and different cohorts overlap.

SMALL-SCALE DISTRIBUTION PATTERN

A "bed" is defined as a circular patch of organisms from a single cohort, whose density falls off with distance from the center. This decline is simulated by a bivariate normal distribution (density gradients along underwater transects of scallop populations follow a bell-shaped contour [see Fig. 2 and Caddy 1970]). Evidently, densities estimated from random population samples rarely follow a normal distribution in nature (Elliott

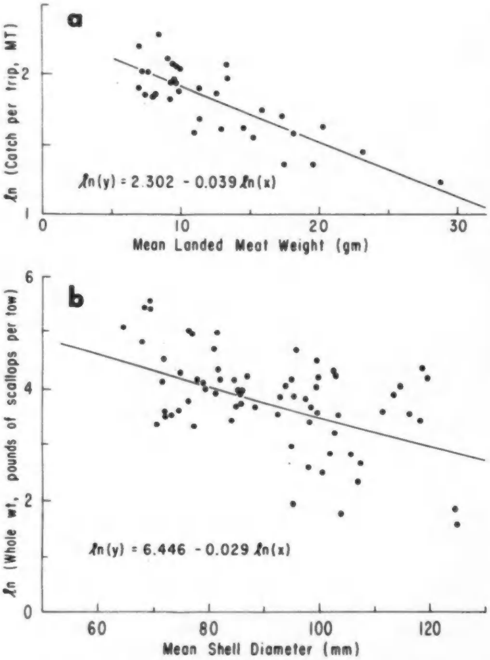


FIG. 4. a) Relation between landed meat weight (g) and catch (MT) per trip for the Canadian fleet: July–Aug. 1970. b) Relation between mean shell diameter and whole weight (1b) of scallops taken in 1-nautical mile tows with an 8-ft offshore dredge (June 1970).

1971), although a bivariate normal is perhaps the best model where random dispersal of recruits from a central point occurs after spawning (Pielou 1969). Whether or not this mechanism, or the bivariate normal have any general validity for large-scale distributions of sedentary organisms, it allows assessment of the effects of contagion on exploitation strategy.

CONSTRUCTION OF THE RECRUIT ARRAY

First consider that the center of the patch of recruits overlies the central square a_{yz} of a matrix X containing S × T unit areas. The distance of any unit area (a_{ij}) from the center of the patch is then given by:

$$x = \sqrt{(s \cdot y - s \cdot i)^2 + (t \cdot z - t \cdot j)^2}$$

where s and t are the unit area dimensions. The number of recruits N_{ijk}' to each unit area a_{ij} is specified by the bivariate normal distribution with equal standard deviations (σ_N) along the i and j axes[2]:

$$N_{ijk'} = \frac{N_T}{2\Pi\sigma^2} \cdot e^{-x^2/2 \cdot \sigma_N^2} \qquad \begin{array}{l} i = 1, 2, \ldots S \\ j = 1, 2, \ldots T \end{array}$$

where N_T is the number of recruits in each patch before biomass constraint.

In order to randomize position of the patch on the ground, the recruit array generated was transferred to an identical matrix X* where the patch center is redefined by uniform random numbers p and g, such that $1 \leqslant p \leqslant S$, and $1 \leqslant g \leqslant T$. To avoid excessive loss of those recruits from X that fall beyond the boundaries of X*, the stratagem used in transferring the recruits to X* was to partition X into four submatrices (see Appendix), and exchange these diagonally (Fig. 6):

$$X = \begin{bmatrix} A_1 & A_2 \\ A_3 & A_4 \end{bmatrix} \rightarrow \begin{bmatrix} A_4 & A_3 \\ A_2 & A_1 \end{bmatrix} = X^*$$

Without this strategem, more patches must be generated to use up the annual recruitment, and the overall recruit distribution approaches uniformity. The recruit density in each unit area of X* is then tested to see that total biomass of all ages does not exceed an upper limit $B_{\max ij}$. The stratagem is then repeated until the annual recruitment is assimilated in X* as a series of overlapping patches.

The number and position of patches of new recruits resulting from this stratagem varies randomly, with the constraint that total recruitment to the matrix remains constant. Although no overall density-dependent recruitment is postulated, a limiting biomass $B_{\max ij}$ defines "available space" for new recruits within each unit area and imposes a local density-dependent relationship between pre- and postrecruits (Hancock 1970).

The distribution of organisms within each unit area is considered uniform, and with progressive reduction of $B_{\max}$ and σ_N^2 individual beds approximate to "discs" containing a uniform population density (Paloheimo and Dickie 1964). In reality, "carrying capacity" of each unit area will be related to its productivity, leading to area-specific values for "virgin" biomass, $B_{\max ij}$ (Table 1C). This incidentally provides a useful way of defining the population geographically. By setting $B_{\max ij}$ to zero, the boundaries of the grounds can be defined (e.g. Fig. 7).

---

[2] The use of unequal standard deviations allows elliptical beds; these were described for shellfish in strong tidal areas (Bullis and Cummins 1961), but are not considered further here.

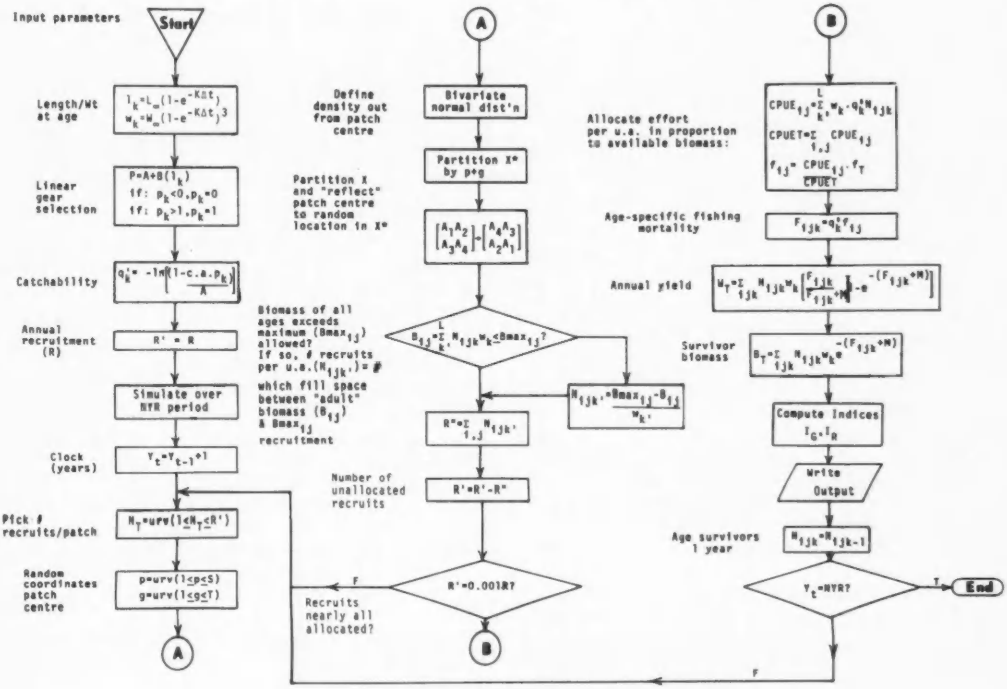

Input parameters
Start
Length/Wt at age
$l_k = L_\infty(1-e^{-K\Delta t})$
$w_k = W_\infty(1-e^{-K\Delta t})^3$
Linear gear selection
$P = A + B(l_k)$
if: $p_k < 0, p_k = 0$
if: $p_k > 1, p_k = 1$
Catchability
$q_k' = -\ln\left[\frac{(1 - c.a.p_k)}{A}\right]$
Annual recruitment (R)
R' = R
Simulate over NYR period
Clock (years)
$Y_t = Y_{t-1} + 1$
Pick # recruits/patch
$N_T = urv(1 \le N_T \le R')$
Random coordinates patch centre
$p = urv(1 \le p \le S)$
$g = urv(1 \le g \le T)$
A
A
Define density out from patch centre
Bivariate normal dist'n
Partition X* by p+g
Partition X and "reflect" patch centre to random location in X*
$\begin{bmatrix} A_1 A_2 \\ A_3 A_4 \end{bmatrix} \rightarrow \begin{bmatrix} A_4 A_3 \\ A_2 A_1 \end{bmatrix}$
Biomass of all ages exceeds maximum ($Bmax_{ij}$) allowed? If so, # recruits per u.a.($N_{ijk'}$) = # which fill space between "adult" biomass (B_{ij}) & $Bmax_{ij}$ recruitment
$B_{ij} = \sum_{k'}^{L} N_{ijk} w_k \le Bmax_{ij}$?
$N_{ijk'} = \frac{Bmax_{ij} - B_{ij}}{w_{k'}}$
$R'' = \sum_{i,j} N_{ijk'}$
Number of unallocated recruits
R' = R' - R"
R' = 0.001R?
F
Recruits nearly all allocated?
B
B
Allocate effort per u.a. in proportion to available biomass:
$CPUE_{ij} = \sum_{k'}^{L} w_k \cdot q_k' N_{ijk}$
$CPUET = \sum_{i,j} CPUE_{ij}$
$f_{ij} = \frac{CPUE_{ij} \cdot f_T}{CPUET}$
Age-specific fishing mortality
$F_{ijk} = q_k' f_{ij}$
Annual yield
$W_T = \sum_{ijk} N_{ijk} w_k \left[\frac{F_{ijk}}{F_{ijk}+M}\right] 1 - e^{-(F_{ijk}+M)}$
Survivor biomass
$B_T = \sum_{ijk} N_{ijk} w_k e^{-(F_{ijk}+M)}$
Compute Indices
I_G, I_R
Write Output
Age survivors 1 year
$N_{ijk} = N_{ijk-1}$
$Y_t = NYR$?
T
End
F

FIG. 5. Schematic flow chart for program YRAREA.

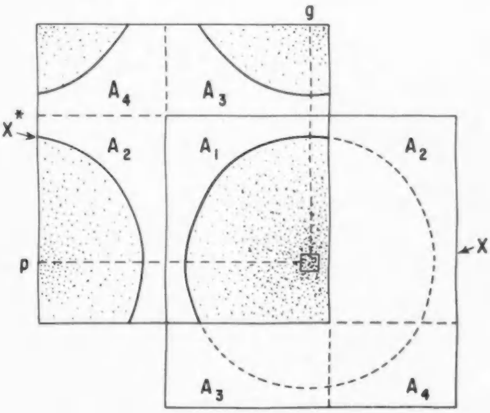

g
A4
A3
X*
A2
A1
A2
p
X
A3
A4

FIG. 6. Strategy used to accumulate patches of new recruits in array X*: each patch in turn is centered on array X, and partitioned by uniform random numbers p and g (see text), submatrices exchanged, and recruits accumulated in X* if maximum biomass constraints are satisfied.

SPATIAL ALLOCATION OF FISHING EFFORT

The whole matrix receives a constant effort (f_T) annually by a single gear type. Effort in each unit area (f_{ij}) is made proportional to local catch per unit effort ($CPUE_{ij}$) at the start of the year. $CPUE_{ij}$ is approximated by the product of population size (N_{ijk}) and catchability (q_k'), summed between the first partially recruited age, k' and the maximum age (L) contributing significantly to the catch, and expressed using age specific values (w_k) in units of weight:

$$CPUE_{ij} = \sum_{k=k'}^{L} w_k \cdot q_k' \cdot N_{ijk}$$

where

$$i = 1, 2 \ldots S$$
$$j = 1, 2 \ldots T$$
$$k = k', k' + 1 \ldots L$$

Summing $CPUE_{ij}$'s over the whole area gives:

$$CPUE_T = \sum_{i}^{S} \sum_{j}^{T} CPUE_{ij}$$

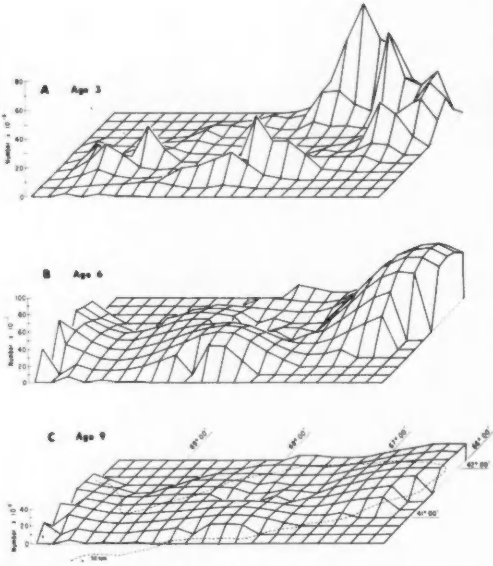


FIG. 7. A) Simulated distribution of 1.25 × 10^6 age 3 recruits over an 11 × 23 matrix of unit areas (Georges Bank) as superimposed bivariate normal distributions ($\sigma^2_{\bar{X}} = 4$). Recruit density constrained by estimated $B_{\max ij}$'s, the whole matrix receiving constant annual recruitment and effort (11,400 days). Effort is distributed in proportion to catchable population per unit area, and the survivors at ages 6 and 9 displayed in Fig. 7B and C (different scales).

If f_T units of effort are stratified by the $CPUE_{ij}$'s, the effort falling in unit area a_{ij} given proportionate allocation is:

$$f_{ij} = \frac{CPUE_{ij}}{CPUE_T} \cdot f_T$$

Given this assumption

$$\frac{f_T}{CPUE_T} = V \text{ (a constant)}$$

under steady-state conditions, and $f_{ij} = V.CPUE_{ij}$. It is evident that this approach to the suballocation of effort is artificial (although perhaps more reasonable than assuming that effort and abundance are independently distributed!). Fishermen are continually reevaluating density gradients, and if perfect information on stock distribution were available at any one time, effort would tend to be exclusively expended on areas of above average density. However, navigational inaccuracy, slow spread of information between vessel skippers, and the desire to explore for more promising areas all disperse effort, while still assuring that high density areas are the most heavily fished. Also, factors other than abundance (e.g. bottom roughness, distance from port) may affect effort distribution, so that for increased realism, a subscripted value (V_{ij}) is estimated that may be considered to represent the probability of a unit of effort falling in a given unit area, assuming uniform abundance. V_{ij} was estimated by:

$$\hat{V}_{ij} = \frac{\bar{f}_{ij}}{\overline{CPUE}_{ij}}$$

where $\bar{f}_{ij}$ and $\overline{CPUE}_{ij}$ are long-term averages for local effort (Table 1B) and catch per unit effort.

On Georges Bank (lat. 42°N, long. 68°W) the most heavily fished areas receive even higher effort than under proportional effort allocation. When applied to Georges Bank scallop stocks, the annual effort allocated to each unit area was therefore defined as:

$$f_{ij} = \left[\frac{\hat{V}_{ij} \cdot CPUE_{ij}}{\sum_i \sum_j \hat{V}_{ij} \cdot CPUE_{ij}}\right] \cdot f_T$$

which takes into account both historical effort distribution, and simulated biomass distribution.

HARVESTING THEORY

The definition of fishing mortality by Baranov (1918) from the effective area swept by gear of known selectivity over a uniformly distributed population of stationary organisms, can be applied to heterogenous populations if the stock can be subdivided into unit areas within which distribution is effectively uniform.

Modifying Baranov's formulation for the number of survivors (N_1) in a body of water after f units of effort with a real intensity of fishing P:

$$N_1 = N_0 (1 - P)^f \quad \ldots\ldots\ldots 1)$$

noting that with a uniform stock distribution, $P = \frac{c.a.p.}{A}$, where a = area swept per day, A = area occupied by the stock, and c and p are the probabilities of capture and retention by the gear, respectively, which can be estimated experimentally (Caddy 1971b). The expression for the number of survivors (N_1) left in area A (neglecting natural mortality) is:

$$N_1 = N_0 \left(1 - \frac{c.a.p.}{A}\right)^f$$

or $$\frac{N_0}{N_1} = \left(1 - \frac{c.a.p.}{A}\right)^{-f} = e^F$$

or
$$F = -f \cdot \ln\left(1 - \frac{c.a.p.}{A}\right) \ldots\ldots 2)$$

Following Beverton and Holt (1956), note that as $\frac{c.a.p.}{A} \rightarrow 0$, F can be expressed by the conventional approximation $F \simeq q' \cdot f$ where $q' = \frac{c.a.p.}{A}$ is the "elemental" catchability coefficient[3] derived from the observed performance of the gear, as opposed to q, the proportionality constant between f and F, when each is estimated independently. The major difficulties that have discouraged the use of elemental catchability coefficients are:

1) obtaining relevant data on gear performance,

2) the nonrandom distribution of animal populations and fishing effort even within statistical unit areas.

Stock distribution within each unit area is still likely to be contagious (Beverton and Holt 1956), thus underestimating mortality by the "area swept" method if the fleet can pinpoint local high densities within unit areas. However, effects of small-scale contagion may be approximated by allowing c, the probability of capture by the gear, to include effects of "aimed fishing."

In this formulation, c will be considered independent of age, but age-specific gear retentions (p_k) defined by a gear selection ogive (Fig. 8). Expressing fishing mortalities separately for each age-group and unit area, equation (1) becomes:

$$_1N_{ijk} = {_0N_{ijk}} \cdot \left(1 - \frac{c.a.p_{k\cdot}}{A}\right)^{f_{ij}}$$

as
$$\begin{aligned} k &= k', k' + 1 \ldots . \mathrm{L} \\ i &= 1, 2, \ldots\ldots\ldots \mathrm{S} \\ j &= 1, 2, \ldots\ldots\ldots \mathrm{T} \end{aligned}$$

and equation 2):

$$\begin{aligned} F_{ijk} &= -f_{ij} \cdot \ln\left(1 - \frac{c.a.p._k}{A}\right) \\ &\simeq f_{ij} \cdot q_k' \end{aligned}$$

where q_k' is an age-specific elemental catchability coefficient.

The survivors at each age per unit area are then given by:

$$_1N_{ijk} = {_0N_{ijk}} \cdot e^{-(F_{ijk} + M)}$$

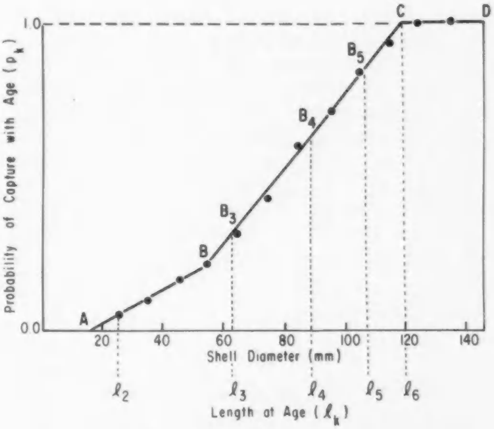


FIG. 8. Linear approximation to selection ogive for offshore dredge given in Caddy (1972), showing age-specific lengths defined by Von Bertalanffy for the Georges Bank scallop stock.

the catch by:

$$C_{ijk} = {_0N_{ijk}} \cdot \left[\frac{F_{ijk}}{F_{ijk} + M}\right] \cdot [1 - e^{-(F_{ijk} + M)}]$$

the residual biomass and annual yield per unit area by:

$$B_{ij} = \sum_{k=k'}^{L} {_1N_{ijk}} \cdot w_k \quad \text{and} \quad W_{ij} = \sum_{k=k'}^{L} C_{ijk} \cdot w_k$$

and the total catch (W_T) and residual biomass (B_T) on the ground by:

$$W_T = \sum_i \sum_j W_{ij} \quad \text{and} \quad B_T = \sum_i \sum_j B_{ij}$$

Finally, the age of survivors is incremented at the end of each year (n):

$$_0N_{k+1,n+1} = {_1N_{k,n}} \; (k = k', k' + 1, \ldots \mathrm{L} - 1)$$

Estimation of Model Parameters for Georges Bank Scallop Population

DYNAMIC POOL YIELD PER RECRUIT APPROXIMATION

Clayden (1972) proposed a discrete version of the Beverton and Holt yield equation using constant annual mortality rates and fixed values for size, weight, and gear retention with age. This formulation allows partial recruitment to be incorporated into the yield equation. However, under nonequilibrium conditions,[4] it cannot be assumed that yield from a population of all exploitable year-classes in 1 yr equals that from a single cohort summed over its life span. Further flexibility is added by converting this to a "real time" simulation in which annual values for the input parameters can be varied. This was achieved by adding R recruits annually over a period $k = 1, 2 \ldots L$ years equal to the life span of the species, and considering that equilibrium yield per recruit is approximated by summing the yield over age in the Lth year.

---

[3] This approximate formulation underestimates q' by only 0.15% using the estimated parameters for the Georges Bank scallop stock; because there is no particular advantage of computation, the detailed formulation is used in program YRAREA.

[4] If dynamic pool assumptions are not met, I assume that an exact definition of "equilibrium conditions" is essentially intractable.

GEAR SELECTION

The population was subject to a constant natural mortality (M = 0.1, Merrill and Posgay 1964), and age-specific fishing mortality rates (F_k) defined from the overall mortality rate (F) by a mesh selection differential, p_k (Walters 1969):

$$F_k = p_k \cdot F$$

p_k was obtained from the length at age, l_k by a segmented linear approximation to the gear selection ogive (Fig. 8) in Caddy (1972):

Thus if: $l_k \leqslant 18$ mm, $p_k = 0.0$
18 mm $< l_k \leqslant$ 55 mm, $p_k = -0.031 + 0.00171\ l_k$
55 mm $< l_k \leqslant$ 119 mm, $p_k = -0.143 + 0.00385\ l_k$
$l_k >$ 119 mm, $p_k = 1.0$

(i.e. first partial retention at $k' = 2$, and full retention at $k = 6$)

Evidently there is culling of the smaller scallops retained, and in later simulations, this cull is assumed to be knife-edged and represented by the selection ogives $l_n B_n C_n D$ (Fig. 8).

For the moment however, it will be assumed that the effective mortalities at age are given by the unmodified selection ogive in Fig. 8.

GROWTH

For comparison with the Beverton and Holt calculation (Fig. 9) the same Von Bertalanffy growth parameters for Georges Bank scallops were used, namely,

$L_\infty = 145.4$
$W_\infty = 46.6$ g: (Brown et al 1972)
$t_0 = 1.5$
$K = 0.38$

and knife-edge selection assumed to apply at age 4 (i.e. for $k < 4$, $p_k = 0.$, otherwise $p_k = 1.0$). The rate of change of yield with F using this discrete approximation closely parallels the Beverton and Holt model, but absolute yield is roughly 10% lower (equivalent to the Beverton and Holt curve with $t_\rho' = 3.75$: Fig. 9). Because yield curves are most often used to describe changes in productivity with fishing effort, the discrete approximation is adequate for most purposes, and this slight discrepancy probably arises from the difference between discrete and continuous formulations of weight at age. The yield curve incorporating linear approximations to the selection ogive closely resembles the Beverton and Holt prediction at $t_\rho' = 3.5$; maximum yield per recruit being reached at F = 0.3, and declining at between 4 and 2% for each further 0.1 increment in F (Fig. 9).

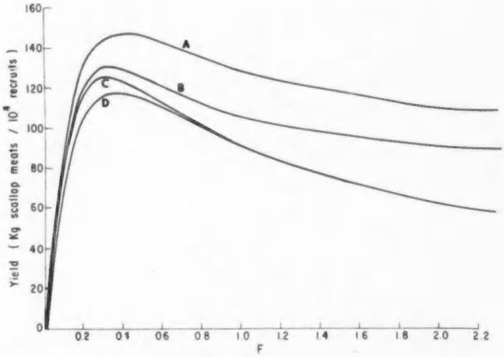


FIG. 9. Different formulations for the dynamic pool yield per recruit relation for Georges Bank scallops (10^4 recruits p.a.; M, K, L_∞, t_0 constant). A) Beverton and Holt formulation ($t_\rho' = 4$, $t_\lambda = 12$); B) Discrete approximation with knife-edge selection at age 4; maximum age, L = 12); C) Discrete approximation with linear selection curve (Fig. 8): (maximum age, L = 12); D) Discrete approximation with linear selection curve (Fig. 8): (maximum age, L = 10).

UNEXPLOITED BIOMASS PER UNIT AREA

The yield per recruit formulation suggests an approximate method of estimating local virgin biomass ($B_{\max_{ij}}$) which takes into account effort expended in each unit area. The ratio of virgin or unexploited biomass to maximum sustained yield $\frac{B_{\max}}{Y_{\max}}$ may be regarded as constant under dynamic pool assumptions (Alverson and Pereyra 1969), and from the relation between yield per recruit and fishing mortality defined above $\frac{B_{\max}}{Y_{\max}} \simeq 9.01$ for the Georges Bank stock. If the same yield per recruit relation applies within all unit areas, and the mean fishing intensity ($q' \cdot \bar{f}_{ij}$) can be defined relative to $q' f_{\max}$ (fishing intensity providing maximum yield per recruit), it is possible to estimate unexploited biomass for each unit area, if the average catch/unit area ($\bar{C}_{ij}$) over a period of years approximates to the equilibrium yield at fishing intensity $q'\bar{f}_{ij}$. Figure 10 represents two of a family of curves relating yield per recruit and biomass to fishing effort for different levels of recruitment. As noted by Beverton and Holt (1957), p. 264, the level of recruitment can be estimated by $\frac{\bar{C}}{Y_w/N_T}$ where $\bar{C}$ is the average weight of catch over a period of years with average annual recruitment N_T and yield Y_w at the same level of fishing intensity. Thus,

$$R_{ij} \simeq \frac{\bar{C}_{ij}}{Y_w/10^4}$$

where Y_w is the calculated yield per 10^4 recruits with fishing mortality $\bar{q}'f_{ij}$.

By simple proportionality from Fig. 10:

$$Y_{\max_{ij}} = \frac{\bar{C}_{ij}}{Y_w} \cdot Y_{\max};$$

and $$B_{\max_{ij}} = \frac{9.01(\bar{C}_{ij} \cdot Y_{\max})}{Y_w}$$

Values of $B_{\max_{ij}}$ obtained in this way for each unit area are given in Table 1C and suggest a virgin biomass for the whole bank of 286,000 MT meats. (This is almost certainly too high, because for the less productive unit areas, only a fraction of the total area supports scallop populations, hence q' is underestimated.)

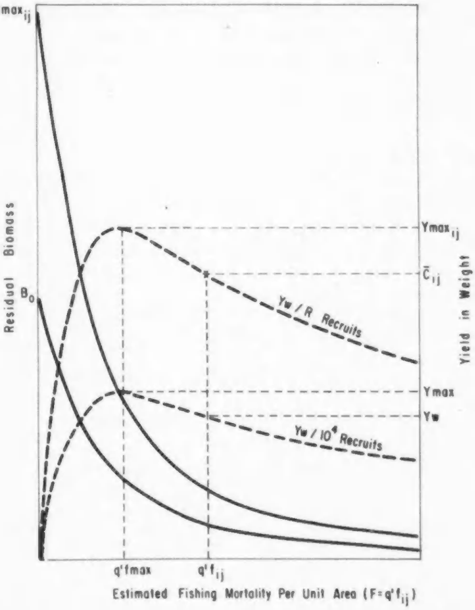


FIG. 10. Diagrammatic representation of method of estimating $B_{\max_{ij}}$. The mean catch per unit area ($\bar{C}_{ij}$) for 1957–58 is assumed to fall on an equilibrium yield per recruit curve for a steady recruitment of R recruits p.a. (Note: residual biomass and yield in weight not to same scale.)

ESTIMATION OF OVERALL MORTALITY AND CULL SIZE

U.S. research vessel surveys in the period 1958–63 suggest an overall value of $F = 0.7$ for the whole bank, corresponding to $\bar{f}_T = 11{,}593$ nominal days fished during the same period, and an overall $q = 6.04 \times 10^{-5}$ (J. A. Posgay personal communication). Using this value, the corresponding level of fishing mortality during the period 1957–68 inclusive was estimated from the nominal effort as $F = 0.64$. A 90–100 mm cull size was in effect during the same period. Since 1969, cull size has fallen to around 80 mm (Brown et al. 1972) in response to a steady decline in stock abundance and a more than threefold increase in landed price (Caddy and Lord 1971). From research vessel surveys, there are now indications that fishing mortality is greatest on 3 yr olds just entering the fishery.

PARAMETERS OF BARANOV'S FISHING MORTALITY FORMULATION

Using $F = 0.64$ for the period 1957–68 inclusive, and detailed information on effort distribution over the same period, the elemental catchability coefficient q' can be obtained by satisfying the equality:

$$F = \ln\left[\frac{\sum_i \sum_j {}_0N_{ij}}{\sum_i \sum_j {}_1N_{ij}}\right] - M = 0.64 \quad \begin{matrix} i = 1, 2 \ldots 11 \\ j = 1, 2 \ldots 23 \end{matrix}$$

where:

$${}_0N_{ij} = \left[\frac{\bar{c}_{ij}(q'\bar{f}_{ij} + M)}{q'\bar{f}_{ij}}\right] \cdot [1 - e^{-(q'f_{ij} + M)}]^{-1}$$

and $${}_1N_{ij} = {}_0N_{ij}\, e^{-(q'f_{ij} + M)}$$

$\bar{c}_{ij}$ and $\bar{f}_{ij}$ are the 11-yr averages of catch and effort for each unit area fished in the period, and $M = 0.1$. A value of $q' = 0.003$ was found by trial and error to give a good approximation to the independent estimate of fishing mortality.

Canadian log book data on hours spent dragging per day can be used to estimate a, the area swept by a standard day's effort. Although there is evidence that during peak abundance years 1960 and 1961, hours dragged/day by the

Canadian fleet fell below average due to the practice of deck loading and stopping to shuck out the catch, in other years, hours fished per day remained fairly constant, averaging 13.8/day. A mean towing speed of 3.75 knots (6.94 km/h) was estimated by Bourne (1964), for two dredges each 3.8 m across the mouth, equivalent to an area swept per standard day of 0.728 km^2, discounting effects of multiple dragging over the same area. A 10′ unit area is 256.5 km^2 and the probability of retention p corresponding to an average size at capture of 110–115 mm is approximately 0.92, judging from Fig. 8. Noting that $q' \simeq \frac{c.a.p.}{A}$, this suggests a value for c of approximately 1.15. This is over 3 times the efficiency of capture (0.3) by the offshore dredge suggested by tag and recapture experiments for scallops over 50-mm shell size (Caddy 1971b). The tentative conclusion is that contagion of fishing effort onto patches within each unit area increases capture efficiency by more than 3 times over the figure predicted for random stock and effort distribution.

Estimated Fishing Mortality Across the Bank

Adopting a value for q' of 0.003, estimates of "typical" fishing mortalities within each unit are given by $F_{ij} = q'\bar{f}_{ij}$. The area-specific fishing mortality rates F_{ij} are above F_{max} (= 0.35 − 0.45) as predicted by the dynamic pool yield per recruit model (Fig. 9C and D) for the areas yielding most of the catch (Fig. 11), and above 2.0 for the most heavily fished unit area. These values, although high, are consistent with the fishing strategy described by Bourne (1964): concentrate effort on an area until it is depleted below the level yielding economic catches before moving to a new locality. Values of F greater than unity (F = 1.18) were confirmed for this area of the bank following a period of good local recruitment in 1970–71 (Caddy 1972). In contrast, predicted values of F_{ij} were below F_{max} for the less productive southern and central Georges Bank.

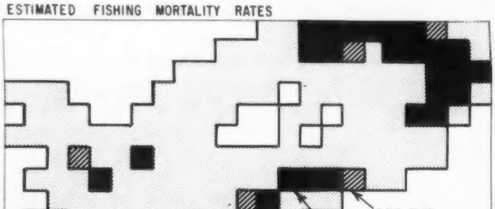


Fig. 11. Fishing mortality rates per unit area estimated for the period 1957–68 from the mean fishing efforts ($\bar{f}_{ij}$: Table 1B) and an elemental catchability coefficient q' = 0.003. Areas being fished at around MSY shaded; "overfished" areas in black; "underfished" areas stippled.

Concentration Indices and Effort Distribution over Georges Bank

Two concentration indices have been proposed to measure the relative distribution of stock density (as local catch per unit effort) and fishing effort. That of Gulland (1955) is defined as:

$$I_g = \left[\frac{\sum_i \sum_j C_{ij}}{\sum \sum f_{ij}}\right] \cdot \left[\frac{1}{N} \cdot \sum_i \sum_j C_{ij}/f_{ij}\right]^{-1}$$

Values of I_g greater than unity (indicating concentration of effort onto high density areas) have been noted by Gulland for North Sea fish stocks, and Calkins (1963) for Pacific tuna. Although effort and catch per unit effort are not statistically independent, the index proposed by Rothschild and Robson (1972) takes the form of a correlation coefficient between spatial distribution of catch per unit effort, and effort for the stock as a whole:

$$I_r = \frac{(a/N) - (b/N)\cdot(c/N)}{\sqrt{\sigma^2_{c/f}\cdot\sigma^2_f}}$$

where

$$a = \sum_i \sum_j C_{ij}; \quad b = \sum_i \sum_j C_{ij}/f_{ij}; \quad c = \sum_i \sum_j f_{ij}$$

and $\sigma^2_{c/f}$ and σ^2_f are the variances of catch per unit effort and effort, respectively. $I_r = 0$ (equivalent to $I_g = 1$) when stock and effort are independently distributed (dynamic pool assumption), but $0 < I_r < 1$ when effort is concentrated onto the stock. The major practical difficulty in applying these indices is choosing the value of N, the number of unit areas containing some part of the stock. Varying N with the number of unit areas fished per year would seem to destroy the descriptive value of the index, but any other number describing a fixed stock area would seem fairly arbitrary.

A number of conflicting estimates are available for the area occupied by scallop stocks on Georges Bank. Fishing was carried out at least once by U.S. or Canadian vessels within 157 10-min unit areas on the bank between long. 66°W and long. 70°W in the period 1957–68 inclusive, equivalent

TABLE 3. Estimated annual variances of catch, effort, and catch per unit effort (U.S. and Canada) by unit area and calculated values for two concentration indices.

Yr	No. unit areas fished	Annual catch (U.S. + Can.)	Spatial variance catch (σ^2_c)	Nominal effort (days) (U.S. + Can.)	Spatial variance of effort (σ^2_f)[a]	Variance of CPUE ($\sigma^2_{c/f}$)[a]	I_g	I_r
1957	120	18588.0	57771.4	11327	20822.5	0.42	1.222	0.251
1958	109	16467.0	42403.3	9947	15599.4	0.55	1.326	0.306
1959	110	22756.5	130057.8	10497	25896.5	0.96	1.287	0.225
1960	109	29083.0	303913.5	10395	34102.1	5.48	1.407	0.136
1961	110	32528.3	218947.7	11473	24624.0	1.48	1.386	0.332
1962	115	34126.9	216171.4	13636	32112.7	1.05	1.293	0.294
1963	115	30739.7	116499.8	13613	21890.6	0.82	1.744	0.684
1964	127	26418.9	54367.6	13176	13411.3	0.55	0.927	−0.169
1965	108	12762.0	44460.1	7837	13406.0	2.57	1.354	0.126
1966	78	13083.3	64501.5	6528	14848.6	1.01	1.993	0.375
1967	92	13672.2	34652.5	8534	12263.2	0.55	1.689	0.476

[a] Calculated assuming stock area ≡ 143 unit areas.

to 12,043 nautical miles^2 (41,306 km^2). This is undoubtedly an overestimate of stock area since it includes peripheral unit areas falling partly outside the boundaries of the bank. Another more reasonable estimate of 10,800 nautical miles^2 (37,043 km)^2 equivalent to 143 units areas each 74.8 nautical miles^2 (256.5 km^2) was measured by planimeter from a chart of areas of the bank that provided some catches during 1944–61 (J. A. Posgay, personal communication). Annual values of I_g and I_r were therefore calculated for 1957–67 using $N = 143$ (Table 3).

An interpretation of fluctuations in these indices requires a brief description of events in the fishery during the period, the most important of which was the heavy recruitment to the bank in 1959–60 which largely supported the fishery over the following 4–5 yr (Caddy and Lord 1971). Peak landings followed this period of peak recruitment by 2–3 yr, and the year of maximal effort lagged behind catches by a further 2 yr, as Canadian investment in the offshore fishery in the early 1960s increased effort on the stocks.

Except for 1960 and 1966, I_r and I_g showed similar behavior (Table 3), all values except for 1964 being above 0 and 1, respectively, suggesting concentration of effort onto high density areas. From 1961 to 1964 as these areas on the productive Northern Edge and Peak were depleted, the fleet increased its effort and area fished: 110 unit areas were fished in 1961, and 127 in 1964. During the same period, both indices fell steadily until by 1964 fishing effort was independent of abundance and perhaps even distributed in areas where abundance was less than maximal. Following depletion of the 1959–60 recruitment, in 1965–66 a large proportion of the Canadian fleet diverted its efforts to grounds off Virginia (ICNAF area 6), and the number of units areas fished fell to 78 as residual effort was again concentrated on the Northern Edge of the Bank. Used in this way, these indices evidently measure the extent to which fishing effort is dispersed from areas of consistently high production to include less productive areas supporting lower population densities.

Predictions of the Model

PROPORTIONAL EFFORT ALLOCATION WITH UNIFORM CARRYING CAPACITY ($B_{\max ij}$)

It is beyond the scope of this study to define true "equilibrium" conditions subsequent to the Lth year, although it is suspected from preliminary runs that yield and biomass stabilize fairly quickly after year L, but oscillations in age-specific mortality continue. It will be necessary here to assume that "typical" values are generated for each set of input parameters in the Lth year of the simulation.

To illustrate the consequences of aimed fishing on a clumped population, a hypothetical situation is postulated where population densities within each unit area may approach a uniform $B_{\max ij}$ (set to 1600 MT/ua) for an 11 × 11 array of unit areas ($\sigma^2_N = 1$, and $L = 8$ yr). A constant recruitment of 2.0×10^9 recruits p.a. is added to the matrix each year; partial recruitment defined as in the selection ogive in Fig. 8, all other parameters are the same as in the dynamic pool model described earlier for the Georges Bank scallop stock. The sequence of mortality rates with age in the Lth year of simulation (Fig. 12) shows progressive departure with increasing effort

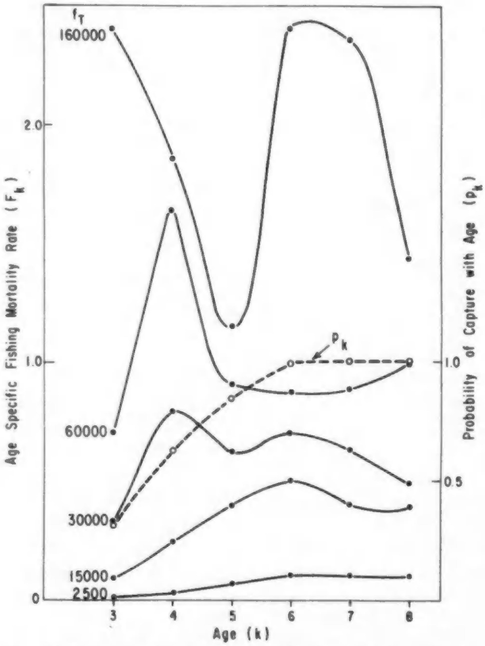


FIG. 12. Smoothed curves showing effects of increasing effort on age-specific mortality in the Lth year of simulation for an 11 × 11 matrix of unit areas (uniform $B_{max_{ij}}$) under proportional effort allocation ($\sigma_x^2 = 1$, L = 8): partial recruitment to the gear as defined in Fig. 8 is included for comparison.

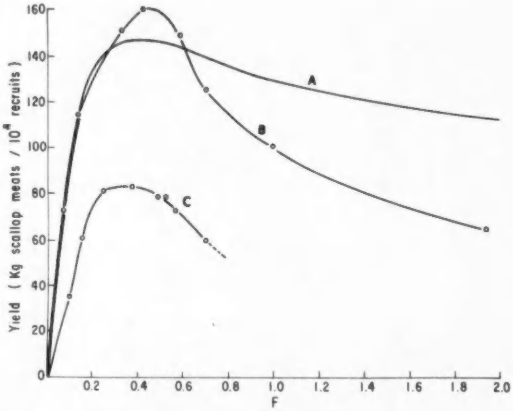


FIG. 13. A comparison of A, the yield per recruit prediction for the Beverton and Holt dynamic pool yield/recruit formulation at different levels of fishing mortality with the yield in the Lth year of simulation for the same parameters; B, under proportional effort allocation (11 × 11 matrix of unit areas, $B_{max_{ij}}$ uniform: $\sigma_x^2 = 1$, L = 8), and C, with an 11 × 23 matrix of unit areas; recruitment and fishing effort being constrained by $B_{max_{ij}}$ and $\overline{V}_{ij}$, respectively.

from that predicted under "dynamic pool" assumptions. At low effort, age-specific mortalities parallel the predefined partial recruitment to the gear, reaching an asymptote at age 6+ and full recruitment. At higher levels with proportional effort allocation, peak mortality occurs on partially recruited year-classes 5 and 4 and for unrealistically high levels of effort, on year-class 3, and subsequently declines. There is the suggestion (from the age distribution arrays) that adjacent year-classes tend to be mutually exclusive spatially, while those separated by a period of years may be jointly occurring. Compared with the Beverton and Holt prediction, yield under proportionate effort allocation peaks at a higher level of mortality (F = 0.5) and subsequently drops off sharply (Fig. 13).

CATCH CURVES UNDER PROPORTIONAL EFFORT ALLOCATION

If the mortality rates generated in the previous section under proportional effort allocation existed in a steady state, the catch curves shown in Fig. 14 for different levels of fishing effort would be realized. Their most striking features are a) that although the inflexion point at low effort levels (f_T = 2500 days) occurs at age 6 (full gear retention), it moves towards the younger ages with increased effort, until at high effort levels it coincides with the age at first partial recruitment, and b) at intermediate effort levels (f_T = 5000–60,000 days) the slope of the catch curve is rather insensitive to change in effort. This also suggests that if samples are averaged from unit areas with different histories of fishing effort, "convex" catch curves such as those described by Ricker (1958) might result.

APPLICATION OF AN AGE-STRUCTURED MODEL TO GEORGES BANK SCALLOP STOCKS

It is quite evident that with the incomplete data base for this fishery, an age structured model cannot be fitted in detail, even if the underlying assumptions for such a model are met. The best approach is to assume reasonable values for input parameters, and search for interrelationships between variables that may be tested explicitly by field observation.

Because of the larger array of unit areas (11 × 23) for the Georges Bank population, it was necessary to assume a maximum age of L = 10 yr when applying YRAREA to Georges Bank scallop

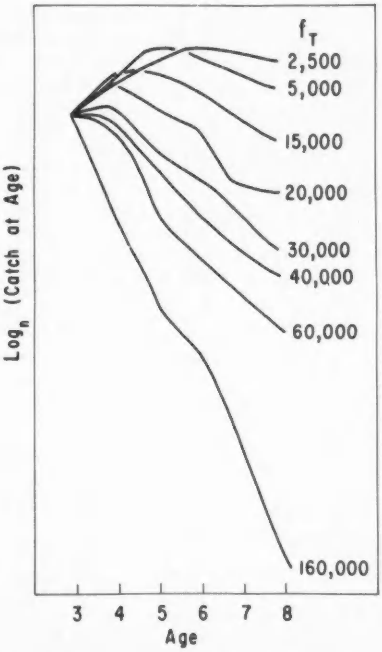


FIG. 14. Shapes of predicted catch curves with steady-state age-specific mortality rates given in Fig. 12 for different levels of effort.

stocks. This is an underestimate since older scallops are caught, but reducing t_λ from 12 to 10 in the dynamic pool simulation has a relatively minor effect on the yield if $F > 0.5$: for lower values of fishing mortality, it reduces Y_{max} by 7%; displacing F_{max} from 0.3 to 0.4 (Fig. 9).

1) *Proportional effort allocation:* $B_{max_{ij}}$ *varied* — For added realism, the model can take into account the fact that ($B_{max_{ij}}$) varies across Georges Bank. Area specific values for $B_{max_{ij}}$ estimated earlier were therefore used to limit recruitment to each unit area.

The 157 unit areas between long. 66°W and long. 70°W which yielded some catches in the period 1957–68 were enclosed in an 11 × 23 matrix of unit areas; $B_{max_{ij}}$ being set to zero for surrounding unit areas in deep water and on Georges Shoal where no significant scallop stocks exist (Table 1C).

The sequence of events during a 10-yr simulation period in which an age structure is built up by addition of 2-yr-old recruits (10^4 p.a.) and effort allocated to each unit area in proportion to realizable catch per unit effort, is illustrated in Fig. 7, which shows arrays of age 3 recruits generated by YRAREA, and their survivors at ages 6 and 9 under proportional effort allocation. The peak areas of recruitment on the Northern Edge have been fished down so that density at age becomes progressively less variable across the bank, and the center of gravity has been displaced southward towards the areas of low carrying capacity. The time sequence of events is illustrated more clearly in Table 4A and B for low and high levels of effort, respectively.

The most obvious difference between the predictions of this and the dynamic pool model, concerns the effects of "availability" of a year-class (availability being determined by the extent to which a year-class distribution coincides with areas of peak population density) on age-specific mortality. For example (Table 4A), the first year-class of 3 yr olds in year 2 being the only year-class in the population appreciably retained by the gear, is subject to a higher fishing intensity than in subsequent years: and in fact at this low level of effort, remained the most heavily fished year-class for the first 5 yr of the simulation. Fishing mortality on younger animals declined with time as later year-classes became available and effort was aimed over a wider spectrum of age-groups. Year-classes that entered the population in years 3 and 4 were subject to the highest mortality towards the end of the L year period, presumably because having been subject to a lower initial mortality than earlier age-groups, their larger contribution to the overall biomass was sufficient to make them the "target" year-classes later in the simulation. There is also the suggestion that a less abundant, older year-class (e.g. ages 8 and 9 in year 10) whose distribution is coincident with the more abundant 5 yr olds, is subject to high "incidental" mortality.

The behavior of the two concentration indices I_g and I_r is different: since by definition, effort was correlated with catch per unit effort, I_r does not deviate appreciably from unity. (This is evidently an artificial situation since such high values are unlikely to be met with in reality.) I_g falls off steadily, stabilizing and rising slightly in the last 3 yr. It is tentatively suggested that the high initial values of I_g result from the concentration of biomass into a relatively few unit areas, when the matrix only contained a few year-classes. Overall yield approached an asymptote towards the end of the 10-yr period, and residual biomass fell in the 10th year, due to complete natural mortality of the oldest cohort.

The sequence of events was essentially similar at higher levels of effort (Table 4B), although in this example with $f_T = 30{,}000$ days, the year-class subject to the highest mortality changed each year after year 3. Once again there was the sug-

TABLE 4. Annual changes in some population variables during a 10-yr simulation period with proportional effort allocation, and 10^4 recruits p.a. Recruit distribution over an 11 × 23 matrix is dictated by a bivariate normal distribution ($\sigma_N^2 = 1$), with local densities constrained by estimated values of $B_{\max_{ij}}$.

Year	Fishing mortality at age (F_k)									Residual biomass	Yield (*kg*)	I_r	I_g
	2	3	4	5	6	7	8	9	10				
					A) *annual effort* = 1,000 *days*								
1	<0.001									2.17	0.02	.999	8.69
2	"	.054								31.61	1.72	.992	7.73
3	"	.008	.088							101.80	6.90	"	5.32
4	"	.008	.027	.083						208.60	11.46	"	3.32
5	"	.004	.024	.041	.059					340.30	15.78	"	2.41
6	"	.003	.016	.037	.045	.049				485.50	19.07	"	1.90
7	"	.002	.011	.029	.042	.038	.037			632.90	21.57	"	1.58
8	"	.003	.009	.022	.037	.036	.031	.029		758.50	23.36	"	1.38
9	"	.003	.014	.019	.031	.035	.031	.027	.024	837.20	24.84	"	1.28
10	"	.003	.014	.036	.032	.035	.036	.030	.026	762.70	26.22	"	1.44
					B) *annual effort* = 30,000 *days*								
1	<0.001									1.77	0.44	.999	8.52
2	"	1.014								11.33	17.24	.959	5.09
3	"	.478	.855							31.03	26.66	.977	2.16
4	"	.431	.905	.571						50.04	48.87	.975	1.84
5	"	.261	.843	.685	.543					69.10	58.47	.969	1.45
6	"	.259	.934	.677	.542	.467				82.12	75.10	.971	1.43
7	"	.190	.795	.761	.656	.481	.500			93.26	79.20	.973	1.30
8	"	.245	.583	.674	.626	.630	.522	.720		107.60	80.56	.982	1.15
9	"	.181	.705	.716	.562	.482	.669	.550	.854	115.10	92.00	.983	1.17
10	"	.258	.703	.700	.641	.465	.430	.895	.779	117.90	97.67	.980	1.18

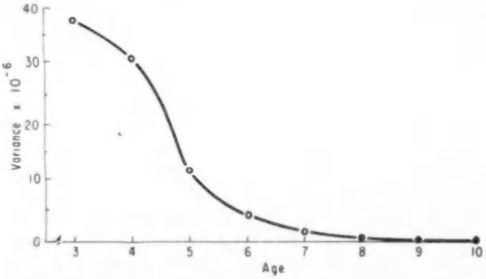


FIG. 15. Predicted trend with age of variance in abundance per unit area. Survivors from an initial population of 10^6 2-ring scallops recruited to an 11 × 23 matrix of unit areas ($B_{\max_{ij}}$ as in Table 4A, $\sigma_N^2 = 4$) are subjected to 11,400 days fishing per year with proportional effort allocation. (See Fig. 7 for typical age-group arrays.)

gestion of "linking" of year-classes 5–6 yr apart with similar patterns of distribution. This phenomenon raises again the question of how equilibrium conditions can be defined in models in which dynamic pool assumptions are not met.

In addition to changes in exploitation rate with age, a steady reduction in population variance with age was seen (Fig. 15), and from the sequence of year-class arrays (Fig. 7) this is seen to be caused by selective fishing of the dense areas of recruitment on the Northern Edge.

2) $B_{\max_{ij}}$ *varied, but effort distribution constrained by* $\hat{V}_{ij}$ — Fishing effort allocated to each unit area may depend on other factors (e.g. distance from port, suitability of terrain for dredging) in addition to potential catch. Area-specific values for $\hat{V}_{ij}$ (the proportionality constant between historical abundance and fishing effort), were calculated for each unit area and used to constrain the effort allocated to each unit area.

The end result of these two constraints are, respectively, that recruitment to the less productive central and southern unit areas cannot exceed a low level, and that fishing effort allocated to the historically more productive areas of the bank exceeds that predicted under proportional effort allocation. These restraints are artificial in that $\hat{V}_{ij}$ will change slightly under different conditions of abundance, and might be more accurately determined with variances by regression of annual values of f_{ij} on $CPUE_{ij}$ for each unit area, rather than by ratios of means.

The relation between yield in the Lth year of

TABLE 5. Effect of increasing effort on population parameters in the Lth year of simulation. 10^4 recruits added per annum, with $\sigma_N^2 = 4$ and $B_{max_{ij}}$ and $\hat{V}_{ij}$ as defined in Tables 4A and B.

f_T	Yield (*kg*)	Residual biomass (*kg*)	I_r	I_g	F_3	F_4	F_5	F_6	F_7	F_8	F_9	F_{10}	$\bar{F}$
1000	35.57	572.70	.793	5.731	.054	.132	.199	.201	.100	.045	.016	.021	.096
2500	60.28	556.50	.725	3.735	.109	.292	.281	.235	.161	.086	.022	.018	.151
5000	80.87	479.70	.589	2.877	.266	.540	.457	.375	.183	.080	.046	.024	.246
10000	82.04	327.60	.418	2.108	.295	.724	.802	.619	.335	.139	.071	.034	.377
15000	79.82	221.60	.395	2.044	.361	.942	1.021	.787	.448	.190	.076	.060	.486
20000	79.45	152.00	.414	2.175	.400	.727	.958	.951	.594	.267	.148	.084	.516
30000	74.75	144.80	.281	1.571	.460	.993	.951	.885	.436	.286	.126	.087	.528
40000	72.64	118.50	.181	1.361	.493	.925	1.140	.880	.516	.303	.144	.098	.562
80000	59.92	60.50	.084	1.151	.743	1.126	.851	.934	1.167	.438	.193	.151	.700

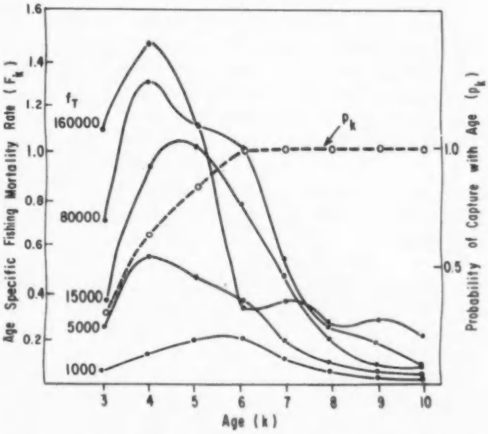


FIG. 16. Smoothed curves showing effects of increasing effort on age-specific fishing mortality rates in the Lth year of simulation for an 11 × 23 matrix of unit areas (Recruitment constrained by $B_{max_{ij}}$: $\sigma_N^2 = 4$, L = 10). Partial recruitment to the gear as defined by the selection ogive in Fig. 8 included for comparison.

the simulation and the arithmetic mean of age-specific mortalities ($\bar{F}$) is shown in Fig. 13C. This suggests that the present yield is considerably below that which would result from proportional effort allocation (Fig. 13B) with the same annual recruitment. An explanation for this may be sought in Table 5 and Fig. 16, which show that fishing mortalities of 8+ ring scallops are well below F_{max} at all but unreasonably high effort levels (presumably because the survivors of these age-groups tend to be on the relatively unfished southern edge of the bank). Conversely, low density scallops on the more productive Northern Edge are fished more heavily than predicted under proportional effort allocation.

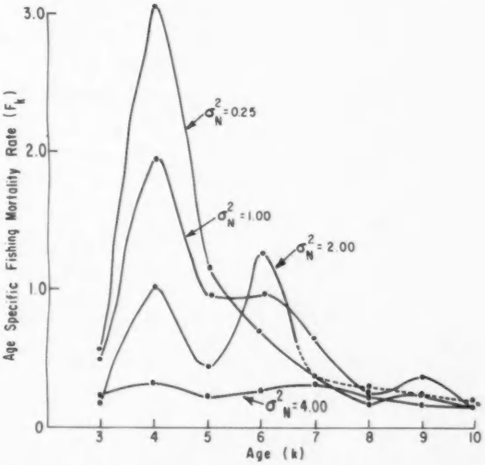


FIG. 17. Smoothed curves showing effect of changes in variance (σ_N^2) of the bivariate normal distribution used in generating the recruit array, on age-specific fishing mortality rates simulated for the Georges Bank population. Effort (f_T = 11,400 days) allocated in proportion to initial catch per unit effort, and recruitment constrainted by $B_{max_{ij}}$.

VARIANCE OF RECRUIT DISTRIBUTION

No obvious way was found to estimate σ_N^2 directly from the limited data on the distribution and shape of scallop patches in the Georges Bank population. If we consider density gradients within a patch to be adequately approximated by a bivariate normal distribution which assumes discrete values for recruit density at the central point of each unit area, then the percentage of the patch population found in the central unit area falls off exponentially with σ_N^2 from 64% of the population for $\sigma_N^2 = 0.25$, to 0.5% for $\sigma_N^2 = 32$.

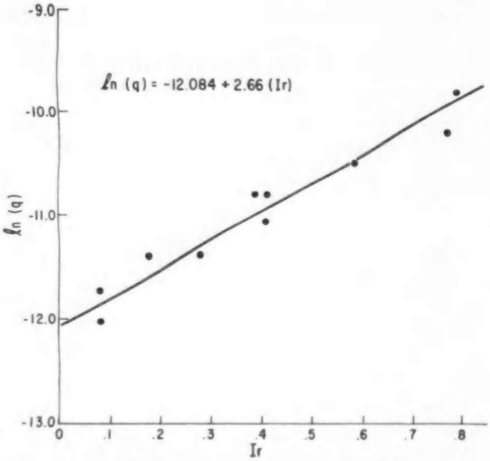


FIG. 18. Relation between overall catchability coefficient for the stock ($q = \overline{F}/f_T$) and the Rothschild and Robson (1972) concentration index (I_r) predicted by simulation.

Simulations show that decreases in σ_N^2 have a similar effect on age-specific mortalities in the Lth year (Fig. 17) to increases in effort with constant σ_N^2; namely that age-specific mortalities become less uniform, and peak mortalities move towards the younger age-classes. At higher values of σ_N^2, age-specific mortalities approximate closely to the dynamic pool prediction.

The patch of new recruits on the Northern Edge surveyed photographically in 1970 and 1971, and a more recent recruitment on the Northeast peak in 1971–72 indicate that most individuals in a patch are contained within 1 or 2 unit areas, and density falls off sharply at the patch periphery. Although further studies of recruitment pattern are evidently needed to establish a realistic value for patch variance, the best approximations are likely to be given by small values of σ_N^2. An arbitrarily chosen value of $\sigma_N^2 = 4$ provided a close approximation to the observed effort array with f_T set at 1957–68 levels (11,400 days fished).

CATCHABILITY COEFFICIENTS AND CONCENTRATION INDICES

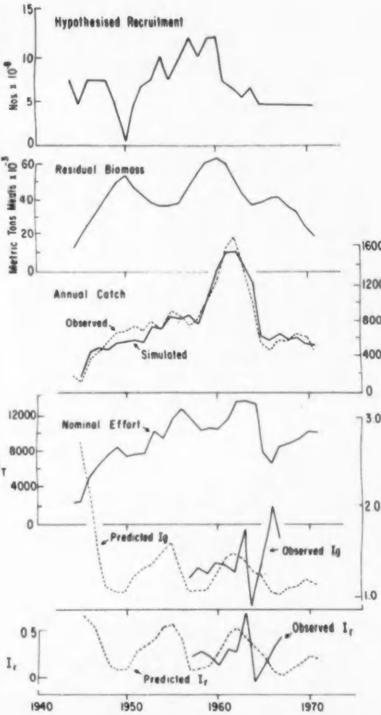


FIG. 19. Simulation of events in the Georges Bank fishery since 1940 using historical effort data and other specified input parameters to YRAREA; annual recruitment varied in order to approximate to the observed historical catch.

Expression of the concentration index I_r in the form of a correlation coefficient between effort and density suggests that the mortality generated by a given level of effort might be higher if it were correlated with stock density rather than independent of it. In other words, some relation might be expected between I_r and q, the overall catchability coefficient relating annual effort to overall mortality. This was explored by comparing predicted values of q and I_r generated by YRAREA; q being defined by $\overline{F}/f_T$ where $\overline{F}$ is the annual mean of the age-specific mortality rates between ages k' and L (Table 5). A log-linear regression of the form $\ln y = a + bx$ was fitted ($r = 0.98$) between the two variables; (Fig. 18):

$$q = 5.649 \times 10^{-6} \cdot e^{2.66\ I_r}$$

Since I_r can be readily calculated if a breakdown of catch and effort by unit areas is available, whereas q is less easily obtained, this suggests a method of correcting annual values of q empirically, at least for changes in spatial distribution of effort.

SUGGESTED CONSEQUENCES OF VARIABLE RECRUITMENT ON EVENTS IN THE GEORGES BANK FISHERY

Any attempt to apply constant recruitment models to the Georges Bank scallop fishery is unlikely to provide an adequate description of events, since from empirical observation, recruitment has been irregular, at least since 1960.

In the absence of explicit data on recruitment, YRAREA and the model parameters derived earlier were used to simulate the observed annual catches from the figures for combined U.S. and Canadian effort (Table 9), by manipulating the level of annual recruitment of 2-yr-old scallops. Because addition of 2 yr olds produces its maximal effects on the catch 2–4 yr later (depending on effort level), simple iteration of recruit level to fit the observed catch in the simulation was impossible and annual recruitment was varied by trial and error: eight trials were carried out before the results in Table 9 were achieved. Because of imprecision in estimation of model parameters, and imperfect fit to observed catches by this method (especially 1948–52 inclusive), this is only a tentative interpretation. However, it provides a reasonable qualitative description of events, and illustrates some interactions between population variables (Fig. 19).

Because there has been a pronounced decline in cull sizes in the commercial fishery since the 1950s, a knife-edged cull of 100 mm was applied from 1945 to 1958 inclusive (equivalent to ogive l_5B_5C D (Fig. 8), and total discard of scallops less than 5 yr old), while from 1959 to 1968 inclusive, l_4B_4C D (equivalent to total discard of scallops 3 yr old or younger) was applied. From 1969 through 1971, a cull of 75 mm (equivalent to ogive l_3B_3C D, and total discard of scallops less than 3 yr old) was used.

The assumption of 100% survival of discards is suspect, but is used in the absence of information on the level of incidental fishing mortality.

The recruitment needed between 1943 and 1948 to reconcile the observed data on catch and effort under the present assumptions, was between 4×10^8 and 7×10^8 individuals per annum. However, events during at least the early years of the simulation are suspect, since during that period population age structure was being built up by incrementing the age of recruits.

The predicted recruitment since 1951 suggests an increase to $1.0\text{–}1.2 \times 10^9$ recruits p.a. between 1956 and 1960 inclusive, but a decline to about 5×10^8 recruits since 1964. This agrees well with previous opinions that a peak in recruitment occurred in this period, although it was thought that above average recruitment had been confined to 2 yr: namely 1959 and 1969.

Both indices I_g and I_r show similar trends in the simulation except for the high initial values of I_g during the early build up of the population age structure. Both show regular fluctuations with peak values for I_r of 0.2–0.6, and I_g of 1.2–1.6 in 1955, 1962, and 1970: the peak index values coinciding with peak landings during those years; index values subsequently declining as effort was dispersed over the bank (Fig. 19).

Agreement between simulated and calculated values of the indices is poor as might be expected in view of present inaccuracies in parameter definition, but the mean values were similar for the period of comparison.

Discussion

GENERAL PREDICTIONS OF THE MODEL

For a sedentary population of organisms showing a contagious recruit distribution limited by some hypothetical maximum density and the existing density of postrecruits, the age-classes generated in successive years will tend to be mutually exclusive in their distribution. If "available biomass" is defined as the sum of catches per unit effort with a given gear selectivity for all year-classes, then within the limits of navigational accuracy of the harvesting units, fishing effort will be concentrated onto peaks in the spatial biomass array. As a first approximation, it is assumed that this fishing strategy can be simulated by allocating fishing effort per unit area in proportion to available biomass. One consequence of these premises is that dynamic pool assumptions no longer apply, and peak mortality at age will occur progressively earlier in the recruited life history as effort and degree of clumping increases. Another consequence is that yield at effort levels higher than that providing maximum sustained yield will drop off more sharply with effort than predicted under dynamic pool assumptions, and variance in catch per unit effort from each unit area will decline with age. A similar trend in peak mortalities towards younger ages for any given effort level is predicted to occur with increased contagion of the population.

Unlike the conventional dynamic pool models, this empirical approach allows for departures of concentration indices I_g and I_r from unity and zero, respectively. It is suggested that I_r may be an index of the catchability coefficient relating total effort to overall fishing mortality for the whole population. Unlike I_r, which seems to adopt fairly constant values with proportional effort allocation, I_g is sensitive to both variance of stock distribution and degree of effort concentration on the stock.

APPLICATION OF THE MODEL TO GEORGES BANK STOCKS

An examination of 1957–68 data on catch and effort for the Georges Bank stock suggests that effort distribution departs significantly from the random hypothesis as judged from the high values of the concentration indices. In fact, areas of high productivity receive even greater effort than predicted from proportional effort allocation, while the converse holds for less productive areas of the bank. One element of caution in the interpretation of catch per unit effort as a measure of abundance is that for a patchy distribution, catch per unit effort may not accurately reflect local abundance if the fleet can locate productive patches within an otherwise unproductive unit area; however, if catch per unit effort within each unit area is an approximate measure of abundance, then the current fishing strategy results in a yield from the bank approximately 40% below that predicted from proportional effort allocation. A hypothesis which could be offered to account for the observed effort distribution is that areas closest to the port of origin (The Great South Channel for New Bedford, and the Northeast Peak for Nova Scotian ports) are fished most heavily because the offshore scallopers make some preliminary tows here on first crossing the 50-fath contour onto the bank, only performing a "random walk" across the more remote and less productive areas of the bank if this preliminary effort is unsuccessful. It seems evident that there is little inducement to travel a greater distance to fish less productive grounds unless the closer, more productive areas are depleted. This makes the concept of effort restriction on the more productive areas an attractive one, if the major problems of enforcement in an offshore area can be overcome.

Events in the Georges Bank scallop fishery over the last 3–4 yr support qualitatively the hypothesis that (at least under conditions of high unit price and low discards), peak mortality occurs progressively earlier with increasing effort. Because of the poor selection properties of the offshore dredge, at least four year-classes (ages 2–4 inclusive) are partially retained, and without any major change in gear design, the dominant year-class in the catches dropped since the early 1960s from age 5 to age 4 for the U.S. fleet (Brown et al. 1972), and to age 3 for at least a proportion of the Canadian fleet (Caddy and Sreedharan 1971). However, for vessels from one Canadian port that fishes predominantly on the less productive areas of the bank, there has been no significant decline in age at capture, indicating that stocks of older scallops still occur at rather low population densities in some areas.

"Elemental" Approaches to Formulation of Fishing Mortality

The formulation of fishing mortality in terms of an area or volume swept per unit effort (e.g. Baranov 1918; Treschev 1973; and this study), although analytically attractive, is likely to seriously underestimate mortality if effects of stock and effort contagion are not taken into account. The approach adopted here of attempting to allow for the effects of contagion using an independent estimate of mortality, and a knowledge of effort expended per unit area is obviously analagous to the standard procedure of defining q for the whole stock as the proportionality constant between independently obtained effort and mortality values. In some ways, a more satisfactory approach would be to define the sampling distribution of catch per unit effort within unit areas and use this to model effects of effort on stock size, but the problems of using this approach with an age-structured population are likely to be horrendously complex.

Potential Applications to other Stocks

It is a well-known phenomenon that with increased levels of exploitation the mean age of the population declines due to the cumulative risk of capture with age, but in general for a population exposed to fishing by a gear in which there is a constant probability of capture with age, the log plot of catch against age subsequent to full retention shows the familiar straight right-hand limb of the catch curve. The occurrence of catch curves which are markedly concave upwards or downwards, e.g. Lofoten cod, Pacific halibut (Ricker 1958) to the right of the inflection, are usually interpreted as resutling from temporal fluctuations in fishing effort or recruitment, or from changes in natural mortality with age. Another possibility suggested by this study is that if year-classes are not homogeneously distributed throughout the population, fishing effort may be concentrated on the more abundant (younger) ages, and mortality may fall off with age even for fully recruited age-groups, or even reach peak values before full retention by the gear. Perhaps more seriously, the slopes of the right-hand limb of the catch curve under proportional allocation are relatively insensitive to changes in effort. It may be noted in this context that an essentially similar prediction was made on different theoretical grounds by Beverton and Gulland (1958) for stocks partially available to fishing.

The strict application of a model designed for sedentary organisms to a migratory fish such as the cod is perhaps as absurd as the application of a dynamic pool model to sedentary species, but as noted by Gulland (1972) for the Iceland cod fishery, in a species where spawning migrations of adult fish occur, seasonal separation of mature and immature fish may take place, allowing for the possibility of "aimed fishing" on different age-groups in the population. In general, it may be postulated for motile species that the three dimensional matrix of ages and areas described in this model in literal geographical terms may be interpreted as a "phase diagram" relating relative availability of year-classes to fishing effort. Some obvious theoretical deficiencies would seem to invalidate its literal application to most fish stocks, but the fact that some of its predictions appear to be supported by data from fish species seems to present a case for the construction of models in which the possibility of age-class separation can occur.

Acknowledgments

I appreciate the Center for Quantitative Science in Fisheries, Forestry, and Wildlife and the Norfish Group, University of Washington, for providing the means and incentive to carry out this study, and in particular, L. Gales who put my feeble programming attempts in workable form, and W. G. Doubleday, P. F. Lett, and V. M. Gallucci who provided valuable advice.

Alverson, D. L., and W. T. Pereyra. 1969. Demersal fish explorations in the northeastern Pacific Ocean — an evaluation of exploratory fishing methods and analytical approaches to stock size and yield forecasts. J. Fish. Res. Board Can. 26: 1985–2001.

Baranov, T. I. 1918. On the question of the biological basis of fisheries. Proc. Inst. Icth. Invest. 1: 81–128.

Beverton, R. J. H., and J. A. Gulland. 1958. Mortality estimation in partially fished stocks. Int. Comm. Northwest Atl. Fish. Spec. Publ. 1: 51–66.

Beverton, R. J. H., and S. J. Holt. 1956. A review of methods for estimating mortality rates in exploited fish populations with special reference to sources of bias in catch sampling. Rapp. P. V. Reun. Cons. Int. Explor. Mer 140: 67–83.

1957. On the dynamics of exploited fish populations. Fish. Invest. Minist. Agric. Fish. Food Ser. II. Fish. 19: 1–533.

Bourne, N. 1964. Scallops and the offshore fishery of the Maritimes. Bull. Fish. Res. Board Can. 145: 60 p.

Brown, B. E., M. Parrack, and D. D. Flescher. 1972. Review of the current status of the scallop fishery in ICNAF division 5Z. Int. Comm. Northwest Atl. Fish. Res. Doc. 72/113: 1–13.

Bullis, H. R. Jr., and R. Cummins Jr. 1961. An interim report of the Cape Canaveral Calico scallop bed. Commer. Fish. Rev. 23(10): 2–7.

Caddy, J. F. 1970. A method of surveying scallop populations from a submersible. J. Fish. Res. Board Can. 27: 535–549.

1971a. Recent scallop recruitment and apparent reduction in cull size by the Canadian fleet on Georges Bank — 1971. Int. Comm. Northwest Atl. Fish. Redbook Part III: 147–155.

1971b. Efficiency and selectivity of the Canadian offshore scallop dredge. Int. Counc. Explor. Sea Shellfish and Benthos Committee paper CM 1971/K 25: 8 p.

1972. Size selectivity of the Georges Bank offshore dredge and mortality estimate for scallops from the northern edge of Georges in the period June 1970 to 1971. Int. Comm. Northwest Atl. Fish. Redbook Part III: 79–85.

Caddy, J. F., and E. I. Lord. 1971. High price of scallop landings conceals decline in offshore stocks. Fisheries of Canada 23(5): 3–7.

Caddy, J. F., and A. Sreedharan. 1971. The effect of recent recruitment to the Georges Bank scallop fishery on meat size landed by the offshore fleet in the summer of 1970. Fish. Res. Board Can. Tech. Rep. 256: 10 p.

Calkins, T. P. 1963. An examination of fluctuations in the "concentration index" of purse-seiners and bait boats in the fishery for tropical tunas in the eastern Pacific, 1951–1961. Inter-Am. Trop. Tuna Comm. Bull. 8: 255–316.

Clayden, A. D. 1972. Simulation of the changes in abundance of the cod (*Gadus morhua* L.) and the distribution of fishing in the North Atlantic. Fish. Invest. Minist. Agric. Fish. Food Ser. II 27(1): 1–58.

Davis, F. M. 1923. Quantitative studies on the fauna of the sea bottom. No. 1 — Preliminary investigations of the Dogger Bank. Fish. Invest. Minist. Agric. Fish. Food Ser. II 6(2): 1–54.

Dickie, L. M. 1955. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin) in the Digby area of the Bay of Fundy. J. Fish. Res. Board Can. 12: 797–857.

Elliott, J. M. 1971. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25: 144 p.

Gulland, J. A. 1955. Estimation of growth and mortality in commercial fish populations. Fish. Invest. Minist. Agric. Fish. Food Ser. II 18(9): 1–46 p.

1972. Population dynamics of world fisheries. Washington Sea Grant Program, Div. Mar. Resour., Univ. Wash., Publ. WSG 72-1, 335 p.

Hancock, D. H. 1970. The relationship between stock and recruitment in exploited invertebrates. Int. Counc. Explor. Sea Symposium on fish stocks and recruitment. Rapp. P. V. Reun. Cons. Int. Explor. Mer 1970: 113–131.

Kristensen, I. 1959. The coastal waters of the Netherlands as an environment of molluscan life. Bacteria 23 (Suppl. 1, VII): 18–55.

Merrill, A. S., and J. A. Posgay. 1964. Estimating the natural mortality rate of the sea scallop (*Placopecten magellanicus*). Int. Comm. Northwest Atl. Fish. Res. Bull. 1: 88–106.

Paloheimo, J. E., and L. M. Dickie. 1964. Abundance and fishing success. Rapp. P. V. Reun. Cons. Int. Explor. Mer. 1964: 152–163.

Pella, J. J., and P. K. Tomlinson. 1969. A generalized stock production model. Inter-Am. Trop. Tuna Comm. Bull. 13: 419–496.

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley Interscience, 286 p.

Posgay, J. A. 1953. The sea scallop fishery, p. 8–24. *In* Sixth Rep. on investigations of methods of improving the shellfish resources of Massachusetts. Commonwealth of Massachusetts, Dep. Nat. Res., Div. Mar. Fisheries.

1957. Sea scallop boats and gear. U.S. Fish. Wildl. Serv. Fish. Leafl. 442: 11 p.

1963. Tagging as a technique in population studies of the sea scallop. Int. Comm. Northwest Atl. Fish. Spec. Publ. 4: 268–271.

RICKER, W. E. 1940. Relation of catch per unit effort to abundance and rate of exploitation. J. Fish. Res. Board Can. 5: 43–69.

1944. Further notes on fishing mortality and effort. Copeia 1: 23–44.

1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

ROTHSCHILD, B. J., AND D. S. ROBSON. 1972. The use of concentration indices in fisheries. U.S. Dep. Commer. Fish. Bull. 70: 511–514.

ROYCE, W. F. 1946. Gear used in the sea scallop fishery Commer. Fish. Rev. 8(12): 7–11.

SAVAGE, R. E. 1956. The great spatfall of mussels (*Mytilus edulis* L.) in the River Conway estuary in spring, 1940. Fish. Invest. Minist. Agric. Fish. Food Ser. II 20(7): 1–20.

SCHAEFFER, M. B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Amer. Trop. Tuna Comm. Bull. 1(2): 25–56.

1957. A study of the dynamics of the fishery for yellow-fin tuna in the eastern tropical Pacific Ocean. Inter-Amer. Trop. Tuna Comm. Bull. 2(6): 245–285.

1968. Methods of estimating effects of fishing on fish populations. Trans. Am. Fish. Soc. 97: 231–241.

TAYLOR, C. C. 1953. Nature of variability in trawl catches. Fish. Bull. 83, Vol. 54: 145–166.

THORSON, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates with special reference to planktonic larvae in the Sound (Øresund). Medd. Dan. Fisk. Havunders. Serie. Plankton 4(1): 523 p.

TRESCHEV, A. I. 1973. Fishing unit measures. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/118: 36 p.

WALTERS, C. J. 1969. A generalized computer simulation model for fish population studies. Trans. Am. Fish. Soc. 98: 505–512.

Glossary of Symbols

(*Note*: *diagonal slash separates two similar symbols and their definitions.*)

γ_{ijk} – The value of any variable γ for age-group k in row i, column j of matrix X^*

γ/γ – Estimated value of γ/long-term average value of γ

a/a_{ij} – Area of seafloor swept by 1 effort unit/ijth unit area (*u.a.*)

$A/A_n/A_{cxa}$ – Area of 1 statistical unit/submatrix n of X^*/submatrix of order *cxa*

$B_T/B_{\max_{ij}}$ – Residual biomass on ground/carrying capacity of unit area a_{ij}

$CPUE_{ij/T}$ – Catch per unit effort (CPUE) in ijth *u.a.*/CPUE summed over matrix

f/F – Fishing effort/annual fishing mortality rate

$f_{\max}/F_{\max}$ – Effort/annual mortality rate giving $Y_{\max}$

g – Uniform random number

I_{bxc} – Identity matrix of order *bxc*

I_g/I_r – Concentration indices after: Gulland/Rothschild + Robson

k'/K – Age at first partial recruitment/Von Bertalanffy growth rate

L – Maximum age contributing significantly to catch

$1_nB_nC_nD$ – Discrete approximation to selection ogive through points 1_n, B_n, C_n, D

M – Annual rate of natural mortality

$N/N_T/{}_0N_{ijk}$ – Number of populated *u.a.*'s on ground/Number of recruits per patch/Initial population of age k in ijth unit area

p/P – Probability of retention by the gear (or random coordinate of patch center)/elemental intensity of fishing

q/q' – Proportionality constant between f and F/"elemental" catchability coefficient

R – Annual recruitment

$s, t/S, T$ – Unit area dimension ($s \times t$)/number of unit areas ($S \times T$) in matrix

$t_0/t_{\rho'}/t_\lambda$ – Parameter of Von Bertalanffy growth equation/Beverton and Holt age at first availability to gear/life span of species

V_{ij} – Probability of 1 unit of effort falling in a_{ij} given uniform biomass over ground

$w_k/W_{ij}/W_\infty$ – Age-specific weight/Weight of catch from A_{ij}/asymptotic weight of Von Bertalanffy growth equation.

$x/X/X^*$ – Distance from center of patch to any point in X/Matrix of unit areas used to create recruit patch/Matrix of unit areas representing fishing ground

$y, z/Y_{\max}$ – Coordinates of central *u.a.* of X^*/Maximum sustainable yield

$\sigma^2_N/\sigma^2_{c/f}/\sigma^2_f$ – Variance of bivariate normal (patch) distribution/variance of catch per unit effort in *u.a.*'s/variance of effort in *u.a.*'s

Appendix

STRATAGEM USED TO RANDOMIZE PATCHES OF RECRUITS ON X*

Matrix X, containing the patch of recruits generated by the bivariate normal distribution around central unit area a_{yz}, is partitioned according to the following rules:[1]

If $S - p > (S - 1)/2$, partition after yth unit area, where $y = p + (S - 1)/2$

If $S - p = (S - 1)/2$, partition after yth unit area, where $y = p$

If $S - p < (S - 1)/2$, partition after yth unit area, where $y = p - (S - 1)/2 - 1$

: and similarly for columns $j = 1, 2, \ldots T$; substituting g for p in the above to give:

$\begin{bmatrix} A_{cxa} & A_{cxb} \\ A_{dxa} & A_{dxb} \end{bmatrix}$ where a–d are the dimensions of the submatrices.

Pre- and postmultiplication by identity matrices results in diagonal exchange of submatrices, and relocation of the central unit area of the patch at a_{pg} in X^*:

$$\begin{bmatrix} O & I_{dxd} \\ I_{cxc} & o \end{bmatrix} \begin{bmatrix} A_{cxa} & A_{cxb} \\ A_{dxa} & A_{dxb} \end{bmatrix} \begin{bmatrix} O & I_{cxa} \\ I_{bxb} & O \end{bmatrix} = \begin{bmatrix} A_{dxb} & A_{dxa} \\ A_{cxb} & A_{cxa} \end{bmatrix} = X^*$$

---

[1] Since S and T are odd numbers, equations for y produce integers.

Metabolism of Pyruvate in Postmortem Adductor Muscle of the Sea Scallop (*Placopecten magellanicus*) During Iced Storage

M. SAKAGUCHI,[1] DORIS FRASER HILTZ, AND W. J. DYER

Department of the Environment, Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S. B3J 2R3

SAKAGUCHI, M., D. F. HILTZ, AND W. J. DYER. 1975. Metabolism of pyruvate in postmortem adductor muscle of the sea scallop (*Placopecten magellanicus*) during iced storage. J. Fish. Res. Board Can. 32: 1329–1337.

Glycolytic metabolic pathways in postmortem adductor muscle of the sea scallop (*Placopecten magellanicus*) during iced storage were studied by means of ^{14}C-pyruvate injected into the muscles. Ion-exchange fractionation of perchloric acid extracts of muscle into cationic, anionic, and neutral components showed that the radioactivity derived from ^{14}C-pyruvate was rapidly incorporated into the cationic fraction during the postmortem storage period. Subsequent ion-exchange chromatography revealed that most of the radioactivity in the cationic fraction was distributed among three major peaks, whose components were identified by paper chromatography as (Peak I) alanine, (Peak II) α-amino-n-butyric acid and an unidentified compound, and (Peak III) octopine. These findings indicate that the disposition of pyruvate in postmortem scallop muscle is mainly via two pathways: transamination to amino acids, and reductive condensation with arginine to octopine. This metabolic pattern in muscles injected immediately after shucking (0-day series) did not differ significantly from that in muscles injected after preliminary storage of the shucked meats for 4 days in ice (4-day series).

SAKAGUCHI, M., D. F. HILTZ, AND W. J. DYER. 1975. Metabolism of pyruvate in postmortem adductor muscle of the sea scallop (*Placopecten magellanicus*) during iced storage. J. Fish. Res. Board Can. 32: 1329–1337.

Les voies métaboliques glycolitiques dans le muscle adducteur du pétoncle géant (*Placopecten magellanicus*) postmortem pendant l'entreposage dans la glace ont été étudiées par injection de ^{14}C-pyruvate dans le muscle. La séparation par échange d'ions d'extraits d'acide perchlorique du muscle en composants cationiques, anioniques et neutres démontre que la radioactivité dérivée du ^{14}C-pyruvate s'incorpore rapidement dans la fraction cationique pendant la période postmortem d'entreposage. La chromatographie par échange d'ions démontre ensuite que la plus grande partie de la radioactivité dans la fraction cationique est répartie parmi trois pics majeurs, dont les composants ont été identifiés par chromatographie sur papier comme étant (pic I) l'alanine, (pic II) l'acide α-amino-n-butyrique et un composé non identifié, et (pic III) l'octopine. Ces découvertes indiquent que le muscle de pétoncle postmortem se débarasse du pyruvate par deux voies métaboliques principales: transamination en aminoacides et condensation réductrice avec l'arginine pour donner l'octopine. Ce schéma métabolique dans des muscles injectés immédiatement après écaillage (série de 0 jour) ne diffère pas significativement de celui de muscles injectés après entreposage préliminaire de 4 jours dans la glace des chairs écaillées (série de 4 jours).

Received February 21, 1975
Accepted April 21, 1975

Reçu le 21 février 1975
Accepté le 21 avril 1975

BIVALVES generally contain a large amount of glycogen in their muscle tissues. The pathways of anaerobic carbohydrate metabolism in these invertebrate species may deviate widely from the classic glycolytic route whereby pyruvate is reduced to lactate, as in fish and mammalian muscle. For example, during anaerobic respiration of intertidal bivalves, the principal end-products of glycogen degradation are alanine and succinate, which arise from the transamination of pyruvate and the carboxylation of phosphenolpyruvate, respectively (e.g. Stokes and Awapara 1968; de Zwaan and van Marrewijk 1973; Hochachka et al. 1973). On the other hand, the metabolic fate of pyruvate in postmortem tissues, which also eventually achieve anaerobic conditions, has been little studied.

Hiltz and Dyer (1971) studied postmortem

---

[1] N.R.C. Postdoctoral Fellow, 1972–73. Present address: The Research Institute for Food Science, Kyoto University, Uji, Kyoto, Japan.

Printed in Canada (J3733)
Imprimé au Canada (J3733)

glycolytic changes in scallop adductor muscle, and found that large amounts of octopine accumulated during iced storage, with comparable decrease in arginine content (see Irvin and Wilson 1939); an active octopine dehydrogenase (van Thoai and Robin 1959), catalyzing the reductive condensation of arginine and pyruvate, was present, and lactic dehydrogenase activity was absent. The possibility of alternate pathway(s) of carbohydrate degradation in this species was suspected, however, as the amount of glycogen degraded postmortem was usually much greater than could be accounted for by octopine production. Hence, delineation of the relative importance of the pathway(s) which may be operative in postmortem scallop muscle was attempted using a radioactive tracer.

The present paper describes the metabolic fate of radioactive pyruvate in postmortem scallop (*Placopecten magellanicus*) meats injected either immediately postmortem or after 4 days preliminary storage of the meats at ice temperature (0 C).

Materials and Methods

Processing, Sampling, and Extraction

Live scallops from the Nova Scotia inshore fishery (Lunenburg area) were held at the laboratory for 20–30 days without feeding in filtered, recirculated sea water at 6–10 C. Upon shucking, the adductor muscles, from which the small attached "catch" muscles were removed, were rinsed with ice-cold 3% sodium chloride solution, drained briefly, and cooled for 5–10 min at 0 C. Several muscles were then injected immediately with radioactive pyruvate (see below), packaged in groups of three muscles to a polyethylene bag, and the bags buried in ice (0-day series). To determine whether the enzymic processes involved in pyruvate metabolism were altered during extended postmortem storage, another lot of muscles was held in ice for 4 days before injection, packaging, and storage as above (4-day series). At intervals during iced storage of the injected meats, three muscles (one bag) of each series were extracted as a single sample with 6% perchloric acid, followed by neutralization of the extracts as previously described (Hiltz and Dyer 1970).

Injection of the Radioactive Compound into the Muscle

Each muscle received 0.4 ml of a radioactive solution containing sodium ^{14}C-pyruvate (UL) 0.96–1.16 μCi (12.5 mCi/mmol, Amersham/Searle), unlabeled sodium pyruvate 71.1 μmol, Tris-HCl 74 μmol (pH 7.1), and sodium chloride 154 μmol. Injections were made with 0.2 ml of the solution at each of two sites in the muscle, schematically shown in Fig. 1.

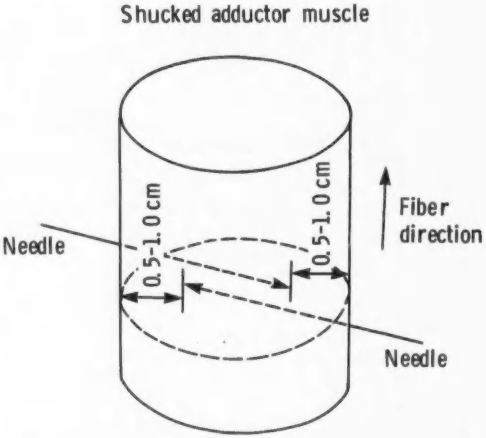


FIG. 1. Sites of injection of radioactive pyruvate into adductor muscles of scallop. Into each site 0.2 ml of ^{14}C-pyruvate solution was injected.

Ion-Exchange Chromatography

Separation of metabolites into cationic, anionic, and nonpolar fractions was achieved by the use of ion-exchange resins, essentially as described by Stokes and Awapara (1968). Neutralized perchloric acid extract (PCA-ext) was applied directly to a column (15 × 0.9 cm) of the cation-exchange resin Dowex 50 × 8 (H^+) 200–400 mesh, followed by washing of the column with water until the effluent was free of radioactivity. The combined effluent and washings (containing the anionic and neutral metabolites) were then applied to a column of Dowex 1 × 8 (Cl^-), 200–400 mesh (15 × 0.9 cm), followed by washing with water as above. The combined effluent and washings from the anion-exchange column made up the neutral fraction.

For further fractionation of radioactive cationic compounds, the latter were recovered from the Dowex 50 × 8 column by eluting with excess amounts of 4 N ammonia followed by subsequent washing with water until the effluent was free of radioactivity. After concentrating under reduced pressure, 1.0–2.0 ml was applied to a Dowex 50 × 8 (100 × 0.9 cm) column equilibrated with 0.1 M citrate buffer (pH 4.20 ± 0.02). Elution was carried out according to the procedure developed by Sakaguchi et al. (1963) for the separation of creatine from fish muscle extractives. The pH of the elution buffer was lowered from 4.25 in the original procedure to 4.20 in the present work to achieve separation of octopine as a single peak. Fractions of 1.2 ml were collected.

For identification by paper chromatography of the compounds in the major cationic peaks, pooled fractions of each peak were concentrated under reduced pressure and applied to Whatman No. 1 paper (12–28 × 46 cm) after desalting. Conditions for descend-

TABLE 1. Distribution of ^{14}C-radioactivity in PCA-ext and PCA-ppt in the muscles injected with ^{14}C-pyruvate 5–10 min after shucking (0-day series) and in muscles injected after 4 days preliminary storage in ice (4-day series).[a]

Storage in ice	PCA-ext				PCA-ppt				Total recovery (%)	
	Radioactivity dpm/muscle ($\times 10^4$)		Recovery[b] (%)		Radioactivity dpm/muscle ($\times 10^4$)		Recovery[c] (%)			
	0-day	4-day	0-day	4-day	0-day	4-day	0-day	4-day	0-day	4-day
0 h	210		93.4		16.6		7.4		100.8	
2	158	147	62.1	69.8	15.6	13.3	6.1	6.3	68.2	76.1
6	178	136	69.6	64.5	13.9	16.1	5.5	7.6	75.1	72.1
12	161	147	62.9	69.8	16.2	16.2	6.3	7.7	69.2	77.5
1 day	143	139	64.0	65.7	10.5	14.0	4.7	6.6	68.7	72.3
2	147	152	65.5	72.1	13.2	20.1	5.9	9.5	71.4	81.6
4	171	165	67.2	78.0	15.8	15.9	6.2	7.5	73.4	85.5

[a] In the 0-day series, 224.1×10^4 dpm of ^{14}C-pyruvate had been injected into each muscle stored for 0 h, 1 day, and 2 days, and 255.1×10^4 dpm into each muscle stored for 2, 6, 12 h, and 4 days. In the 4-day series, 211.2×10^4 dpm was injected into each muscle. The average weight of each muscle was 28.9 g, with a range of 26.5 –31.9 g (0-day series), and average 28.9 g, range 27.5–30.3 g (4-day series).

[b] Radioactivity found in PCA-ext/radioactivity injected into the muscle × 100.

[c] Radioactivity found in PCA-ppt/radioactivity injected into the muscle × 100.

ing development and detection of spots are described under the appropriate figures in the text.

RADIOACTIVITY MEASUREMENT

^{14}C-radioactivity was determined with a Packard Tri-Carb Model 2003 liquid scintillation counter. The scintillation cocktail (15 ml per vial) was composed of toluene-dioxane-ethylcellosolve (1:1:1, vol/vol), and contained 7.5% (wt/vol) naphthalene, 0.4% (wt/vol) PPO (2,5-diphenyloxazole), and 0.01% wt/vol) POPOP (1, 4-bis-2-(5-phenyloxazolylbenzene). To dissolve perchloric acid-insoluble matter (PCA-ppt) in the scintillation cocktail, the solubilizer Packard Soluene 100 was used. Efficiency of counting was determined by the channel-ratio method (Herberg 1965). For measuring radioactivity in the eluate following ion-exchange chromatography of cationic compounds, 0.5 ml was taken from each tube, added to 10 ml of the liquid scintillation cocktail described above, and then counted for 10 min. Radioactivity on paper chromatograms was measured by cutting the dried strips (31 × 4 or 36 × 4 cm) into 2-cm sections crosswise, and counting these in vials containing 10 ml of the cocktail and 0.5 ml Soluene 100 diluted 2-fold with dioxane and ethyl cellosolve (1:1, vol/vol).

OCTOPINE DETERMINATION

Octopine in neutralized perchloric extracts of muscle was determined by the method described previously (Hiltz and Dyer 1971).

Results

The relative proportions of radioactivity incorporated into acid-soluble extracts (PCA-ext) and into PCA-insoluble material (PCA-ppt), in both the 0-day and 4-day series at various time intervals up to 4 days of iced storage, are given in Table 1, along with the overall recoveries of radioactivity injected. In both series, the extracts contained consistently over 90% of the total radioactivity in the PCA-ext + PCA-ppt. Recoveries of radioactivity injected ranged from 68 to 75% for the 0-day series and 72–86% for the 4-day series with the exception of the 0-h sample (0-day), for which the recovery was 100%.

The distribution of radioactivity among cationic, anionic, and neutral fractions of the neutralized PCA-exts, and the change therein during storage of scallop muscle in ice, are given in Table 2 for both the 0-day and 4-day series. In both series, the radioactivity found in the cationic fraction increased rapidly up to 2 days, with little or no further change to 4 days. Radioactivity in the anionic fraction decreased reciprocally with increase in the cationic fraction, with 9–13% remaining at 2 days. The neutral fraction at 0 h in the 0-day series unexpectedly contained a high proportion of radioactivity (10%), which then decreased to 3–4% at 2 days. In the 4-day series, the proportion of radioactivity in the neutral fraction fluctuated between 4.8 and 8.4% throughout the storage period.

The marked change during storage in the amount of radioactivity incorporated into the cationic fraction is illustrated in Fig. 2; the rate of incorporation appears to be only slightly

TABLE 2. Change in the distribution of ^{14}C-radioactivity among cationic, anionic, and neutral fractions during ice storage of scallop muscle in the 0-day series (injected 5–10 min after shucking) and the 4-day series (injected after 4 days preliminary storage of the muscles in ice).

Storage in ice	Dpm applied on Dowex 50 (×10^2)	Dpm passed through Dowex 50 (×10^2)	Dpm passed through Dowex 50 (%)[a]	Dpm applied on Dowex 1[b] (×10^2)	Dpm passed through Dowex 1 (×10^2)	Dpm passed through Dowex 1 (%)[a]	Cationic fraction (%)[c]	Anionic fraction (%)[c]	Neutral fraction (%)[c]
				0-day series					
0 h	340	335	98.5	119	12.3	10.3	1.5	88.4	10.1
2	287	235	81.9	115	14.0	12.1	18.1	72.0	9.9
6	345	258	74.8	182	14.1	7.7	25.2	69.0	5.8
12	300	148	49.3	148	14.8	10.0	50.7	44.4	4.9
1 day	262	77	29.4	135	12.5	9.3	70.6	26.7	2.7
2	320	51	15.8	104	19.9	19.1	84.2	12.8	3.0
4	377	61	16.2	180	43.4	24.1	83.8	12.3	3.9
				4-day series					
2 h	710	671	94.5	431	29.6	6.9	5.5	88.0	6.5
6	299	224	74.9	114	7.3	6.4	25.1	70.1	4.8
12	261	152	58.2	57	6.6	11.6	41.8	51.5	6.7
1 day	179	67	37.4	67	15.0	22.4	62.6	29.0	8.4
2	296	54	18.2	54	20.0	37.0	81.8	11.5	6.7
4	307	46	15.0	38	15.1	39.7	85.0	9.0	6.0

[a] Ratio of dpm passed through to dpm applied to the ion-exchange resins.

[b] Solution containing radioactive compounds was applied to Dowex 1 after having been passed through Dowex 50.

[c] Percent of dpm's in the original PCA extract applied to Dowex 50.

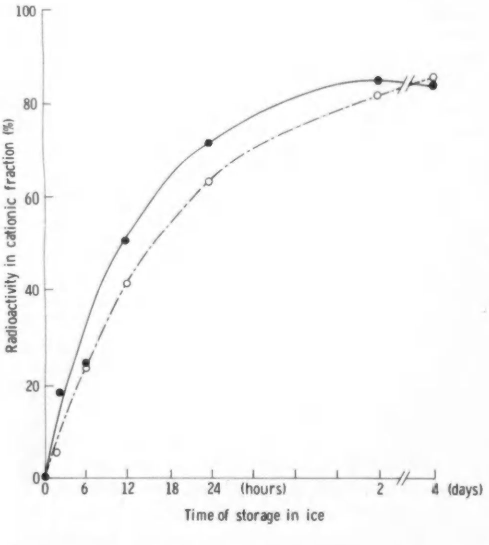


FIG. 2. Rate of incorporation of radioactivity from ^{14}C-pyruvate into the cationic fraction of neutralized PCA-extracts of scallop muscle during storage of the muscle in ice. The scallop meats were injected 5–10 min after shucking (0-day series, ●) or after 4 days preliminary storage in ice (4-day series, ○).

slower in the 4-day series than in the 0-day series up to 2 days storage.

Ion-exchange chromatography of the components of the cationic fraction on 100-cm columns of Dowex 50 yielded three major radioactive peaks (designated P_I, P_{II}, and P_{III}) and two or more minor peaks, a pattern common to all extracts of both the 0-day and 4-day series (Fig. 3). Over 90% of the radioactivity applied to the columns was recovered, and, of this, 76–89% was located consistently in the three major peaks (Table 3). The radioactivity in each of the three major peaks, as a percentage of that in the original PCA-extracts from which the cationic fractions were isolated, increased appreciably with time of storage of the muscle in ice (Fig. 4), although both rate and extent of incorporation of radioactivity differed between the 0-day and 4-day series. In the 0-day series, the rate of incorporation of radioactivity into both P_I and P_{II} was faster than in the 4-day series; incorporation into P_{III}, however, was similar in both series, and virtually complete after 12 h storage, although the amount incorporated was considerably greater in the 4-day series. Changes in intra- and extracellular conditions such as pH and nucleotide and cofactor concentrations during the preliminary 4 days storage in ice before injection of the 4-day series, may explain some of these differences.

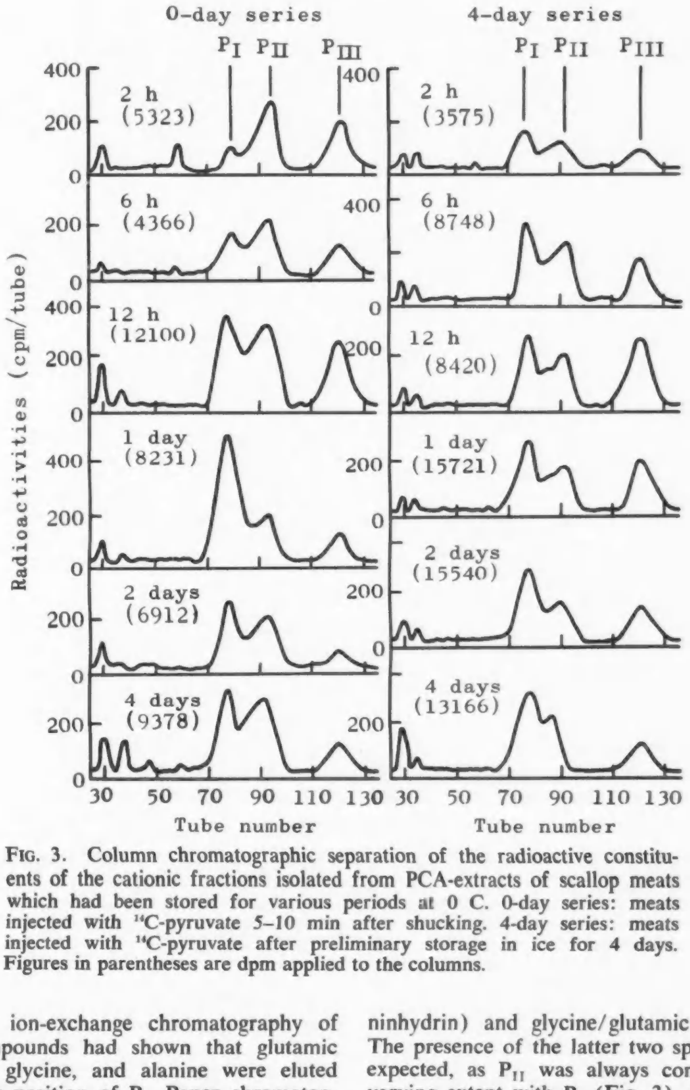


FIG. 3. Column chromatographic separation of the radioactive constituents of the cationic fractions isolated from PCA-extracts of scallop meats which had been stored for various periods at 0 C. 0-day series: meats injected with ^{14}C-pyruvate 5–10 min after shucking. 4-day series: meats injected with ^{14}C-pyruvate after preliminary storage in ice for 4 days. Figures in parentheses are dpm applied to the columns.

Preliminary ion-exchange chromatography of authentic compounds had shown that glutamic acid, proline, glycine, and alanine were eluted together in the position of P_I. Paper chromatography of P_I along with known markers, followed by a ninhydrin spray, gave three spots, two of which were clearly identified as glycine and alanine, and the third, weakly, as glutamic acid (Fig. 5). No proline spot could be detected. Radioactivity was found only in the alanine spot. Paper chromatography of P_{II} revealed three ninhydrin spots; one of these had the same R_f (0.44) as α-amino-n-butyric acid, and the other two ran in the positions of alanine (a faint blue color with ninhydrin) and glycine/glutamic acid (Fig. 6). The presence of the latter two spots was not unexpected, as P_{II} was always contaminated to a varying extent with P_I (Fig. 3). Radioactivity in P_{II}, however, was detected at the same positions at which the ninhydrin spots appeared (Fig. 6). As paper chromatography of P_I had shown that radioactivity had not been incorporated into either glycine or glutamic acid, this suggests that the radioactive spot from P_{II} in the position of glycine/glutamic acid is in fact another compound which has not been identified in the present study. The small amount of radioactive alanine present in the P_{II} chromatogram probably rep-

TABLE 3. Distribution of ^{14}C-radioactivities in the three major peaks obtained by ion-exchange chromatography of the cationic fractions in the 0-day and 4-day series.[a]

Storage in ice	Dpm applied on column (× 10²)	Dpm found in Peak I			Dpm found in Peak II			Dpm found in Peak III			Peak I + Peak II + Peak III	
		(× 10²)	(%)	(%)[b]	(× 10²)	(%)	(%)[b]	(× 10²)	(%)	(%)[b]	(%)	(%)[b]
						0-day series						
2 h	64.9	5.8	8.9	1.6	29.0	44.7	8.1	20.9	32.1	5.8	85.7	15.5
6	53.2	14.2	26.7	6.7	18.9	35.4	8.9	14.1	26.5	6.7	88.6	22.3
12	147.6	38.1	25.8	13.1	49.1	33.3	16.9	37.3	25.3	12.9	84.4	42.9
1 day	100.4	33.4	33.3	23.5	29.0	28.9	20.4	14.3	14.2	10.0	76.4	53.9
2	84.3	20.4	24.2	20.4	34.6	41.0	34.5	9.4	11.1	9.3	76.3	64.2
4	144.4	30.4	26.6	22.2	42.6	37.3	31.3	14.4	12.6	10.6	76.5	64.1
						4-day series						
2 h	43.6	10.2	23.4	1.3	17.5	40.1	2.2	9.1	20.9	1.1	84.4	4.6
6	106.7	24.6	23.1	5.9	33.0	30.9	7.8	30.0	28.1	7.1	82.1	20.8
12	102.7	19.2	18.7	7.8	31.5	30.7	12.8	40.8	39.7	16.6	89.1	37.2
1 day	191.7	45.2	23.6	14.8	48.7	25.4	15.9	60.2	31.4	19.7	80.4	50.4
2	189.5	61.8	32.6	26.6	55.0	29.0	23.7	48.3	25.5	20.8	87.1	71.1
4	160.6	51.7	32.2	27.4	42.9	26.7	22.7	36.1	22.5	19.1	81.4	69.4

[a] The area of P_I was calculated by doubling the left half of the peak. The area of Peak II was calculated by subtracting the area of P_I from the combined areas of P_I and P_{II}.

[b] dpm in each peak as percent of that in the original PCA-extract (the proportion of radioactivity in the cationic fractions relative to that in the PCA-ext (Table 2) has been taken into account in the calculations).

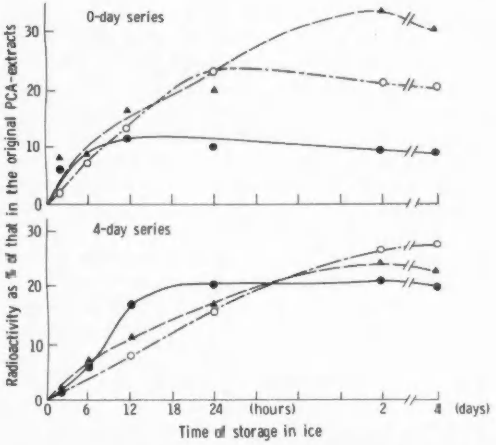


FIG. 4. Incorporation of radioactivity from ^{14}C-pyruvate into the major peaks obtained by ion-exchange chromatography of the cationic fraction of PCA-extracts of scallop muscle during storage of the injected muscles in ice. (○, Peak I; ▲, Peak II; ●, Peak III)

resents that which remained unreacted after treatment with GPT. No valine spot was detected in P_{II}. Paper chromatography of P_{III} gave a single pink spot with Sakaguchi's reagent, that corresponded to authentic octopine (Fig. 7), and that contained a large amount of radioactivity.

Determination of octopine content in the scallop muscle during storage of both series in ice (Table 4) indicated a slower rate of postmortem accumulation of this glycolytic end product than found previously in several lots of iced muscles examined, where levels of 25–35 μmol/g had been reached by 6–10 days (Hiltz and Dyer 1971). In the present work, only about 8 μmol/g of octopine had accumulated after 4 days storage (0-day series), suggesting a rate characteristic of animals captured in the spawning season (Hiltz and Dyer 1971).

Discussion

Of the radioactivity from ^{14}C-pyruvate that was recovered after PCA extraction of the injected scallop muscle, almost all was found in the acid-soluble fraction (PCA-ext), with only 4.7–9.5% in the insoluble portion (PCA-ppt). The latter may represent ^{14}C-pyruvate adsorbed on the denatured protein or present in the adhering fluid, or possibly may indicate incorporation into protein-bound amino acids.

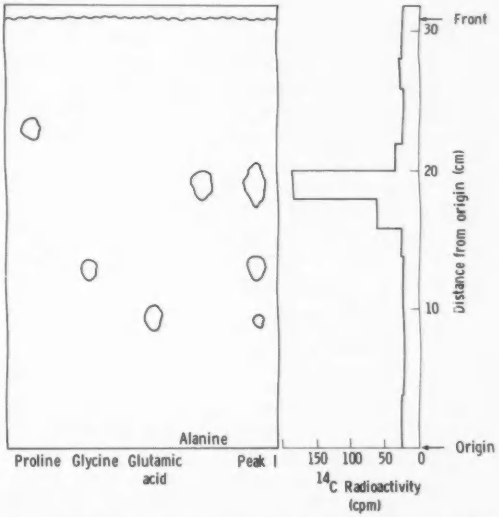


FIG. 5. Paper chromatogram of Peak I (see Fig. 3) showing ^{14}C-radioactivity incorporated into alanine. The composite sample applied was taken from tubes 72–79 of the 2-, 6-, 12-, and 24-h column chromatographic runs in the 0-day series (see Fig. 3). Descending development was carried out with phenol-water = 80:20 (vol/vol) at room temperature for 15 h. Spots were detected with ninhydrin.

The percentage of radioactivity recovered of that injected was somewhat low, 68–75% in the 0-day series, except for complete recovery at 0 h, and 72–85% in the 4-day series. This suggests a leakage of radioactivity from the muscles into the polyethylene bags in which the muscles were contained during storage. The lower recovery, suggesting higher leakage, in the 0-day series may be the result of the pressure exerted by rigor mortis contraction associated with the extensive metabolic activity occurring in scallop muscle within the first 4 days postmortem; Hiltz and Dyer (1971) reported extensive degradation of ATP and arginine phosphate, with concomitant accumulation of octopine and substantial decrease in muscle pH within 4 days storage of scallop meats at 0 C.

The rate of incorporation of radioactivity into the cationic fraction was quite rapid during the early storage period, with 50% conversion to cationic compounds within 12 h of injection in the 0-day series. The rate of incorporation in scallops iced 4 days before injection was only slightly slower (42% conversion by 12 h), suggesting that the enzymic mechanisms responsible for pyruvate metabolism were little affected by the extensive postmortem glycolysis, nucleotide degradation, and fall in pH which normally occur during the first 4 days of iced storage (Hiltz and Dyer 1971).

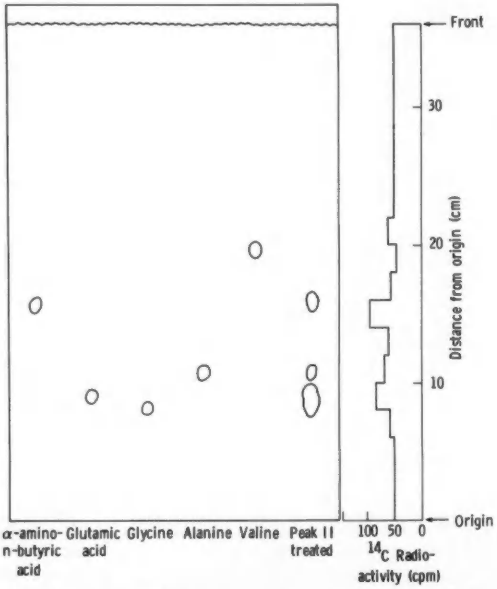


FIG. 6. Paper chromatogram of Peak II (see Fig. 3) showing ^{14}C-radioactivity incorporated into α-amino-n-butyric acid and an unidentified compound. The composite sample applied was collected from tubes 84–96 of the 2-, 6-, and 12-h column chromatographic runs in the 4-day series. It was submitted to paper chromatography after treatment with glutamatepyruvate transaminase and lactic dehydrogenase (Pfleiderer 1963) for 1 h at room temperature to remove excess amounts of alanine with which the peak was contaminated. Descending development was carried out with n-butanol-acetic acid-water = 120:30:50 (vol/vol) at room temperature for 14.5 h. Spots were detected with ninhydrin.

Radioactivity remaining in the anionic fraction at 4 days can probably be accounted for by unmetabolized pyruvate, and possibly by a small incorporation into organic acids, e.g. succinate, and phosphorylated sugars. Incorporation into lactate seems unlikely in view of the lack of LDH activity in extracts of scallop muscle (Robin and van Thoai 1961; Hiltz and Dyer 1971).

Identification of the major components of the cationic fraction showed that radioactivity from injected ^{14}C-pyruvate was incorporated mainly into amino acids such as alanine, α-aminobutyric acid and an unidentified compound, and into octopine. The amount of radioactivity incorporated into amino acids (Peaks I and II) after 4 days storage of the 0-day series was about 5 times greater than that incorporated into octopine and, after 4 days storage of the 4-day series, about 2.6 times greater (Table 3). The incorporation of radioactivity from injected pyruvate ultimately into alanine suggests an active alanine aminotransferase in postmortem scallop muscle, and

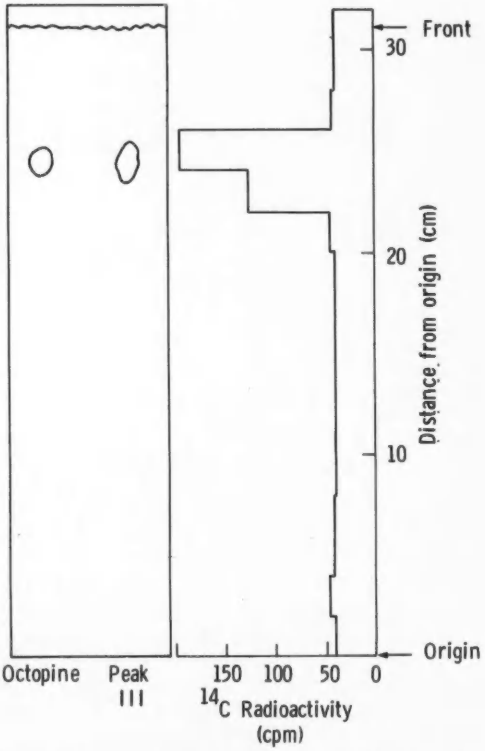


FIG. 7. Paper chromatogram of Peak III (see Fig. 3) showing ^{14}C-radioactivity incorporated into octopine. The composite sample applied was collected from tubes 116–126 of the 12-h column chromatographic run in the 4-day series. The conditions of development were the same as described in the footnote of Fig. 6. Spots were detected with Sakaguchi's reagent.

TABLE 4. Accumulation of octopine in scallop adductor muscle stored in ice.

Storage in ice	0-day series µmol/g	4-day series µmol/g
0 h	1.4	—
2	2.0	10.3
6	2.3	11.3
12	3.4	14.4
1 day	4.0	14.8
2	5.7	18.6
4	8.6	19.9

hence, a metabolic pathway for disposition of pyruvate similar to that reported for intertidal bivalves during anaerobiosis (Hochachka et al. 1973). The route whereby radioactivity from ^{14}C-pyruvate was incorporated into α-aminobutyric acid, a major constituent of P_{II}, is obscure; the unknown compound, also a major constituent of P_{II}, remains to be identified. Incorporation of radioactivity into octopine was not unexpected in view of the relatively large amounts of this metabolic end product that have been found to accumulate in scallop meats postmortem (Hiltz and Dyer 1971). The incorporation into octopine, however, reached a maximum after about 12 h storage of the iced meats in both the 0-day and 4-day series (Fig. 4), although the octopine content of the iced meats continued to increase gradually up to 8 days (Table 4). The apparent cessation of radioactive incorporation into octopine early in the storage period may be the result of a rapid dilution of ^{14}C-pyruvate with native pyruvate supplied by glycogen breakdown during postmortem storage. The amount of pyruvate metabolized during 4 days storage of the iced meat may be estimated from the octopine concentrations to be about 80 μmol/g (8 μmol/g of octopine formed; 10% of the radioactivity incorporated into octopine) and 50 μmol/g for the 0-day and 4-day series, respectively (data from Tables 3 and 4). The estimated total of 130 μmol/g of pyruvate metabolized during 8 days storage would represent a glycogen loss of 65 μmol/g (as glucose) via the phosphorolytic (Embden–Meyerhof) pathway. Decreases in glycogen content of this magnitude have been encountered in various lots of scallop meats during iced storage (Hiltz and Dyer 1970 and unpublished data). It is not known to what extent, if any, glycogen in postmortem scallop muscle may be metabolized amylolytically.

We had reported previously (Hiltz and Dyer 1971) that, in some lots of scallop meats examined postmortem, maximum octopine production (25–35 μmol/g) accounted for only about 20–25% of the glycogen degraded. This discrepancy was reduced further (to about 50% of the glycogen degraded) by our subsequent finding of hexose monophosphate accumulation in scallop meats postmortem (Hiltz and Dyer 1973). The present work indicates that alanine, α-aminobutyric acid, and an unidentified basic compound may also accumulate as end products of postmortem carbohydrate catabolism in this species, although actual concentrations of these metabolites in the scallop muscle during iced storage were not determined. It is clear, however, that the postmortem metabolic fate of pyruvate in scallop muscle is primarily via transamination to amino acids and reductive condensation with arginine to octopine. The carboxylation route leading to succinate from phosphoenolpyruvate (PEP) via PEP-carboxykinase, a major pathway for glucose catabolism in many marine bivalves under anoxic conditions (Hochachka et al. 1973), or from pyruvate via pyruvate carboxylase, does not appear to be involved to any significant extent, if at all, in postmortem glycolysis of scallop muscle.

Acknowledgments

We are grateful to Mr F. C. Read, National Sea Products, Lunenburg, N.S. for his assistance in obtaining live scallops.

de Zwaan, A., and W. J. A. van Marrewijk. 1973. Anaerobic glucose degradation in the sea mussel (*Mytilus edulis* L.) Comp. Biochem. Physiol. 44B: 429–439.

Herberg, R. J. 1965. Channel ratio method of quench correction in liquid scintillation counting. Packard Tech. Bull. 15: 8 p.

Hiltz, D. F., and W. J. Dyer. 1970. Principal acid soluble nucleotides in adductor muscle of the scallop (*Placopecten magellanicus*) and their degradation during postmortem storage in ice. J. Fish. Res. Board Can. 27: 83–92.

1971. Octopine in postmortem adductor muscle of the sea scallop (*Placopecten magellanicus*). J. Fish. Res. Board Can. 28: 869–874.

1973. Hexose monophosphate accumulation and related metabolic changes in unfrozen and thawed adductor muscle of the sea scallop (*Placopecten magellanicus*). J. Fish. Res. Board Can. 30: 45–52.

Hochachka, P. W., J. Fields, and T. Mustafa. 1973. Animal life without oxygen: basic biochemical mechanisms. Am. Zool. 13: 543–555.

Irvin, J. L., and D. W. Wilson. 1939. Studies on octopine. II. The precursor of octopine in autolyzing scallop muscle. J. Biol. Chem. 127: 575–579.

Pfleiderer, G. 1963. L-alanine, determination with glutamate-pyruvate transaminase and lactic dehydrogenase, p. 378–380. *In* H. U. Bergmeyer [ed.] Methods of enzymatic analysis. Verlag Chemie, GMBH. Weinheim/Bergstr. and Academic Press, New York and London.

Robin, Y., and N. van Thoai. 1961. Métabolisme des dérivés guanidylés. X. Métabolisme de l'octopine: son rôle biologique. Biochim. Biophys. Acta 52: 233–240.

Sakaguchi, M., M. Hujita, and W. Simidu. 1963. Studies on muscle of aquatic animals. XXXVII. Separation and determination of creatine and creatinine. Bull. Japan. Soc. Sci. Fish. 29: 531–536.

Stokes, T. M., and J. Awapara. 1968. Alanine and succinate as end products of glucose degradation in the clam (*Rangia cuneata*). Comp. Biochem. Physiol. 25: 883–892.

van Thoai, N., and Y. Robin. 1959. Métabolisme des dérivés guanidylés. VIII. Biosynthèse de l'octopine et répartition de l'enzyme l'opérant chez les invertébrés. Biochim. Biophys. Acta 35: 446–453.

Relative Importance of Food and Water in Long-Term Zinc^{-65} Accumulation by Marine Biota

W. C. RENFRO,[1] S. W. FOWLER, M. HEYRAUD, AND J. LA ROSA

International Laboratory of Marine Radioactivity, Musée Oceanographique, Principality of Monaco

RENFRO, W. C., S. W. FOWLER, M. HEYRAUD, AND J. LA ROSA. 1975. Relative importance of food and water in long-term zinc^{-65} accumulation by marine biota. J. Fish. Res. Board Can. 32:1339–1345.

Shrimp, crabs, and fish were maintained for 3 mo in a ^{65}Zn-labeled simulated ecosystem in which individuals were allowed to accumulate the radiotracer either directly from the water or from a combined food and water pathway. Shrimp and crabs, receiving ^{65}Zn from the food-water milieu, did not attain significantly higher ^{65}Zn body burdens than those individuals that accumulated the isotope from water only. For fish, the food pathway accounted for only 2.5 times more ^{65}Zn than that obtained after direct accumulation from water. Specific activity measurements of both organisms and water as well as comparisons of radioactive concentration factors with those based on stable element measurements indicated that ^{65}Zn in organisms had not reached isotopic equilibrium with the isotope in the water, even though net ^{65}Zn accumulation in shrimp and crabs had ceased by the end of the experiment. It was concluded that there are zinc pools within adult organisms that exchange only slowly, if at all, with zinc atoms available in the organisms' food or surrounding water. Hence, aquatic organisms such as those used in this study can most likely achieve true isotopic equilibrium only after living significant portions of their actively growing life stages in a radioactive environment.

RENFRO, W. C., S. W. FOWLER, M. HEYRAUD, AND J. LA ROSA. 1975. Relative importance of food and water in long-term zinc^{-65} accumulation by marine biota. J. Fish. Res. Board Can. 32: 1339–1345.

Nous avons maintenu durant 3 mois des crevettes, des crabes et des poissons dans un écosystème simulé marqué au ^{65}Zn, dans lequel on a permis aux individus d'accumuler le traceur radioactif soit directement de l'eau, soit par une voie métabolique nourriture–eau combinées. Les crevettes et les crabes recevant le ^{65}Zn du milieu nourriture–eau n'accumulent pas dans leur corps une charge de ^{65}Zn significativement plus élevée que ceux qui l'accumulent à partir de l'eau seulement. Chez les poissons, la voie métabolique nourriture ne rend compte que de 2.5 fois plus de ^{65}Zn que le niveau atteint après accumulation directe à partir de l'eau. Les mesures d'activité spécifique à la fois des organismes et de l'eau, de même que les comparaisons des facteurs de concentration radioactive avec ceux d'éléments stables indiquent que le ^{65}Zn dans les organismes n'atteint pas un équilibre isotopique avec l'isotope de l'eau, même si l'accumulation nette de ^{65}Zn dans les crevettes et les crabes a cessé à la fin de l'expérience. Nous en concluons qu'il y a, à l'intérieur des organismes, des quantités de zinc avec échange très lent, si tant est qu'il y ait échange, avec les atomes de zinc disponibles dans la nourriture des organismes ou dans l'eau environnante. Il en ressort que des organismes tels que ceux qui ont servi à cette étude peuvent en toute probabilité atteindre un véritable équilibre isotopique seulement après avoir passé une partie importante de leurs stades de croissance active dans un milieu radioactif.

Received March 7, 1975
Accepted April 22, 1975

Reçu le 7 mars 1975
Accepté le 22 avril 1975

THE relative importance of the food vs. the water pathway as a source of radionuclides to aquatic organisms has been a point of controversy among radioecologists for some time (Hoss 1964; Polikarpov 1966; Baptist and Lewis 1969; Lowman et al. 1971; Pentreath 1973a, b, c). The two pathways for radionuclide and corresponding stable element accumulation are inseparable in nature; however, most studies attempting to solve this problem have utilized laboratory experiments that treat the two pathways separately. One problem inherent in this approach is to assure that the radionuclide concentrations available to organisms by each separate pathway are available in the same relative proportions as would be the case in

---

[1] Present address: Northeast Utilities Company, Environmental Programs Branch, Hartford, Conn. 06101, USA.

Printed in Canada (J3756)
Imprimé au Canada (J3756)

the natural environment in which the presence of the food does not alter the specific activity of the isotope in the water. The fact that the design of some experiments has not taken this into consideration has led to conflicting results. In addition, many experiments have been so short that comparison of animals in isotopic equilibrium with the radionuclide available to them in their ambient medium was precluded.

Considering the foregoing, an experiment was designed to allow two groups of animals to accumulate radioactivity directly from water and from the combined food and water pathways simultaneously in the same simulated ecosystem. This approach has the advantage of treating the two groups in exactly the same manner, thereby eliminating variation inherent in separate experiments. In this case the only variable was assumed to be the presence or absence of radioactivity in the organisms' food. The purpose of this long-term study was to learn if the accumulation of ^{65}Zn through the food pathway has a significant effect on the total radiozinc level in marine organisms approaching isotopic equilibrium with the radioisotope in their surrounding sea water.

Materials and Methods

In order to simulate an ecosystem in which biotic and abiotic factors would not alter the radionuclide specific activity, a large polyethylene tank was filled with 300 liters of cotton-filtered sea water to which were added 900 μCi of high specific activity ^{65}Zn Cl_2.

The sea water was enriched with 6 mg $NaNO_3$/liter, 3.6 mg Na_2HPO_4/liter, and 0.1 mg $FeCl_3$/liter to promote the growth of phytoplankton already present in the water. The tank, covered with a thin sheet of transparent plastic and located in a sheltered outdoor enclosure, was generally shaded; however, some direct sunlight reached the water during parts of the day. Twelve polyvinylchloride (PVC) cylindrical containers, approximately 20 cm in diameter and 30 cm long with nylon screen at their lower ends, were suspended in the tank to contain the experimental animals. Into each container were placed a single fish of the genus *Gobius*, a small crab (*Carcinus maenas*), and a small benthic shrimp (*Lysmata seticaudata*). To avoid predation the two crustaceans were each contained in individual perforated plastic tubes (4 × 7.5 cm). In two other PVC containers brine shrimp (*Artemia salina*) and mussels (*Mytilus galloprovincialis*) were maintained to serve as a radioactive food source for one group comprised of six experimental animals. Brine shrimp and mussels for use as nonradioactive food were maintained under conditions similar to their radioactive analogs. Two air stones were placed on the bottom of the tank to assure aeration and good water circulation.

The design of the experiment was as follows. All animals were allowed to accumulate ^{65}Zn from water under the same conditions. One group of six animals was allowed to ingest radioactive food, while the other group was fed nonradioactive food. Periodically, all animals were removed from the tank, rinsed, radioanalyzed, and placed in similar PVC containers suspended in nonradioactive sea water at the same temperature, to be fed either radioactive or nonradioactive food rations. All animals were fed 3 times a week during a 3-h period. Each fish received approximately 0.5 g of chopped mussel or several dozen *Artemia* during a feeding period. One half of a mussel shell with the adhering soft parts was placed in each crab container. The shrimp, held in small jars containing nonradioactive sea water, received a predetermined number of *Artemia*. Generally, most of the food ration was consumed within the allotted time; however, crustaceans that were nearing molt usually ate nothing. Radioanalyses of animals receiving nonradioactive food showed that almost no radiozinc was lost during the 3 h they spent out of the radioactive sea water.

After each feeding period the animals were replaced in the radioactive sea water for further uptake. At frequent intervals the crustaceans were observed and any molts present were monitored for ^{65}Zn activity. At the same time water temperatures were recorded.

Artemia were occasionally added to the cultures in the radioactive sea water to assure a sufficient supply at each feeding period. All *Artemia* used as radioactive food were held in the tank of ^{65}Zn-spiked sea water for at least 5 days, an exposure time sufficient to achieve a plateau in ^{65}Zn uptake. The mussel supply in both radioactive and nonradioactive containers was sufficiently large to last the entire experiment. Samples of both *Artemia* and *Mytilus* were also monitored during the experiment to follow the accumulation of ^{65}Zn.

Throughout the 3 mo, salinity was monitored and maintained at 37.9‰ by additions of distilled water. To correct for rapid losses of ^{65}Zn from the water by adsorption to the walls, accumulation by animals, and adsorption to settling particulate matter such as fecal pellets, the ^{65}Zn activity in the water was periodically compared to a reference standard and when water levels decreased significantly, more radioisotope was added to the system. Loss of ^{65}Zn from water was most rapid over the first few days of the experiment but diminished considerably with time. The particulate fraction of ^{65}Zn in the water was also assessed at certain times during the experiment. Particulate ^{65}Zn was defined as that fraction retained on the upper filter after filtering seawater samples through a double layer of 0.45-μ membrane filters. The ^{65}Zn activity in the lower filter was subtracted from that of the upper filter to account for ionic ^{65}Zn sorbed during filtration. Experimental organisms as well as seawater samples collected at the beginning and end of the experiment were measured for stable zinc by anodic stripping voltametry to compare specific activities of water and organisms.

Radioactivity measurements on seawater samples and living experimental animals were performed with a single channel analyzer connected to a well-type

NaI(T1) scintillation crystal (7.6 × 7.6 cm). The use of an internal reference standard permitted correction for ^{65}Zn decay as well as drift of the instrument during the experiment. Overall counting error was estimated to be below 1%. All ^{65}Zn concentrations in the experimental animals are reported as percentages of the ^{65}Zn standard on a per gram wet weight basis or as a concentration factor based on the ^{65}Zn concentration in the sea water.

Stable zinc concentrations of all organisms were measured by anodic stripping voltametry following wet digestion of dried tissue. Concentrations of stable zinc in seawater samples were measured directly without treatment.

Results and Discussion

Six *Mytilus*, which were considered representative of the group of mussels used for food, were counted periodically over the 96-day accumulation period. Figure 1 shows ^{65}Zn was taken up relatively rapidly over the first 20 days after which time accumulation was much slower. After day 60, no net accumulation was observed, indicating that steady state between the exchange of ^{65}Zn in the mussel and water had been reached. Mean concentration factors averaged 175 during this period. Despite an obvious lack of particulate matter in the water on which the mussels could feed, five of the animals showed little, if any, loss of weight during the experiment; however, one individual lost 19% of its wet weight over the 96-day period.

Measurements of ^{65}Zn in aliquots of *Artemia* taken from the tank showed that they rapidly accumulated the isotope and appeared to approach a steady state with ^{65}Zn in the water within 48 h.

The results of the ^{65}Zn accumulation experiments for the two different treatments are presented in Fig 2. In the case of shrimp (Fig. 2a) that were fed radioactive *Artemia*, there was no significant increase in ^{65}Zn body burden over that of shrimp that obtained ^{65}Zn only from the water. Radioanalysis of a single food ration indicated that individual shrimp, by consuming all the *Artemia* presented, could receive from 11 to 50% of their own ^{65}Zn body burden at each feeding. If assimilation of ingested ^{65}Zn by shrimp were high, it would be expected that in these animals radiozinc concentration would increase more rapidly than in animals that had accumulated the isotope only from water. Since this was not the case, it can only be concluded that much of the ingested ^{65}Zn was excreted, perhaps in the form of fecal pellets. Indeed, tests showed that shrimp that had eaten ^{65}Zn-labeled *Artemia* were higher in radiozinc just after the 3-h feeding period than following 24 h after being replaced in the radioactive ecosystem.

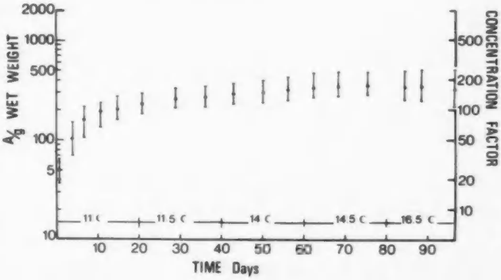


FIG. 1. Accumulation of ^{65}Zn by *Mytilus galloprovincialis*. Each point represents a mean of six animals. Bars indicate the range of values. A = ^{65}Zn in mussel expressed as a percentage of the standard. Mean water temperatures are given along the abscissa. Mussels averaged 3.53 ± 0.69 g wet weight.

It was thought that perhaps the manner in which the *Artemia* incorporated ^{65}Zn might have affected the efficiency with which the shrimp assimilated ^{65}Zn from *Artemia*. If ^{65}Zn accumulation by *Artemia* was principally from water, as was thought to be the case in our experiments, perhaps much of the radionuclide was adsorbed to unassimilable exoskeletal tissue of *Artemia*, hence lowering ^{65}Zn assimilation by shrimp. To test this hypothesis shrimp were fed either a single ration of *Artemia* that had grazed on a dense suspension of ^{65}Zn-labeled phytoplankton, or *Artemia* that had accumulated the radioisotope directly from water. Loss of ^{65}Zn by the two groups of shrimp during the next several days indicated that the fractions of ^{65}Zn excreted were identical; thus, effects due to differences in labeling the *Artemia* used as food were ruled out.

Although values for ^{65}Zn and stable zinc varied widely among the shrimp analyzed at the end of the experiment, ^{65}Zn specific activities were quite similar (Table 1). Unfortunately, a statistical test of the significance of the ^{65}Zn specific activity differences was precluded by the fact that only two individuals in the group accumulating ^{65}Zn from water survived to the end of the experiment.

The large variation among ^{65}Zn body burdens of shrimp in both groups was primarily due to loss of the isotope at molt. Shrimp molted, on the average, every 3 wk and lost approximately 45% of their body burden with each molt. The relatively large difference in ^{65}Zn content between the two groups at day 56 (Fig. 2a) was due to the fact that the three shrimp remaining in the "water uptake" group had all molted just prior to this measurement, thus reducing the mean
]

TABLE 1. Final mean ^{65}Zn specific activities in the experimental organisms.

^{65}Zn uptake pathway	Shrimp	Crabs	Fish
	(nCi ^{65}Zn/μg Zn)		
Water	44.6	31.4	0.7
Food and water	54.1	70.6	3.6
Student's *t*-test (5% level of significance)	—	not significant	significant

^{65}Zn body burden substantially. Clearly, frequent molting can markedly affect zinc accumulation kinetics in shrimp.

A slightly different case was observed with crabs (Fig. 2b). Depending upon the time during the experiment, crabs received, at each feeding, labeled food containing from 35 to 50% of their ^{65}Zn body burden. In general, crabs obtained higher ^{65}Zn body burdens from food and water than from water. The differences, however, were substantial only until the end of the second month. After this time, with the onset of higher water temperatures, the crabs began to molt, losing an average of 61% of the ^{65}Zn body burden with each molted exoskeleton. After the commencement of molting, net ^{65}Zn accumulation slowed considerably and the mean concentrations of radiozinc in both groups were not significantly different. At apparent steady state, the group accumulating ^{65}Zn from water reached a mean concentration factor of approximately 150. The mean ^{65}Zn specific activities at the end of the experiment, although differing by more than a factor of two, were not statistically different at the 5% probability level (Table 1).

In contrast to the crustaceans, the presence of radioactive food in the diet of fish significantly increased the ^{65}Zn body burden over similar animals accumulating the nuclide from water (Fig. 2c). Depending upon the type of food and the time during the experiment, fish could ingest from 17 to 400% of their ^{65}Zn body burden at each feeding. It did not appear that ^{65}Zn steady state was reached in either group during the 3-mo period. When the remaining animals were sacrificed on day 88, the difference in specific activities was statistically significant at the 5% level of significance (Table 1).

On the first day of the experiment, before the animals were introduced, approximately 8% of the ^{65}Zn activity in the water was associated with particles that were retained on 0.45-μ membrane filters. This fraction dropped to 2% by the second day and thereafter remained less than 1% despite repeated ^{65}Zn additions throughout the experimental period. It was felt that the relatively large fraction of particulate ^{65}Zn present on day 1 may have been due to adsorption of the radioisotope to iron particles caused by the addition of $FeCl_3$ in the nutrient enrichment medium. The presence of the particulate fraction was accompanied by a relatively rapid decrease of ^{65}Zn from the water over the first 2 days, possibly caused by precipitation of the particulate iron. This loss in ^{65}Zn activity was compensated by the addition of radiozinc on day 3. Thereafter, ^{65}Zn loss from the water was much more gradual necessitating only occasional, small additions of radiotracer.

Table 2 shows the results of specific activity measurements of water samples taken on the first and last day of the experiment. The fivefold increase in stable zinc indicated the possibility of contamination. The additions of high specific activity ^{65}Zn added a total of only 5.5 μg stable Zn/liter (as carrier) over the 96-day period. Unfortunately, the water was analyzed only twice for stable zinc. However, it is suspected that the contamination took place during a strong windstorm 1 wk prior to termination of the experiment. The tank was uncovered on several occasions during this time and the probability of dust and fine particles entering the water was high. Zinc contamination in laboratory tanks from dust has been noted previously by Kameda et al. (1970).

FIG. 2. Accumulation of ^{65}Zn by (a) shrimp (*Lysmata seticaudata*), (b) crabs (*Carcinus maenas*), and (c) fish (*Gobius*). (□) = mean value for group accumulating ^{65}Zn from food and water pathway; (●) = mean value for group accumulating ^{65}Zn from water only. Bars indicate the range of observations. A = ^{65}Zn in animal expressed as percentage of the standard. Mean water temperatures are given along the abscissa. Shrimp, crabs, and fish averaged 0.23 ± 0.05, 2.90 ± 0.50 , and 4.72 ± 0.92 g wet weight, respectively.

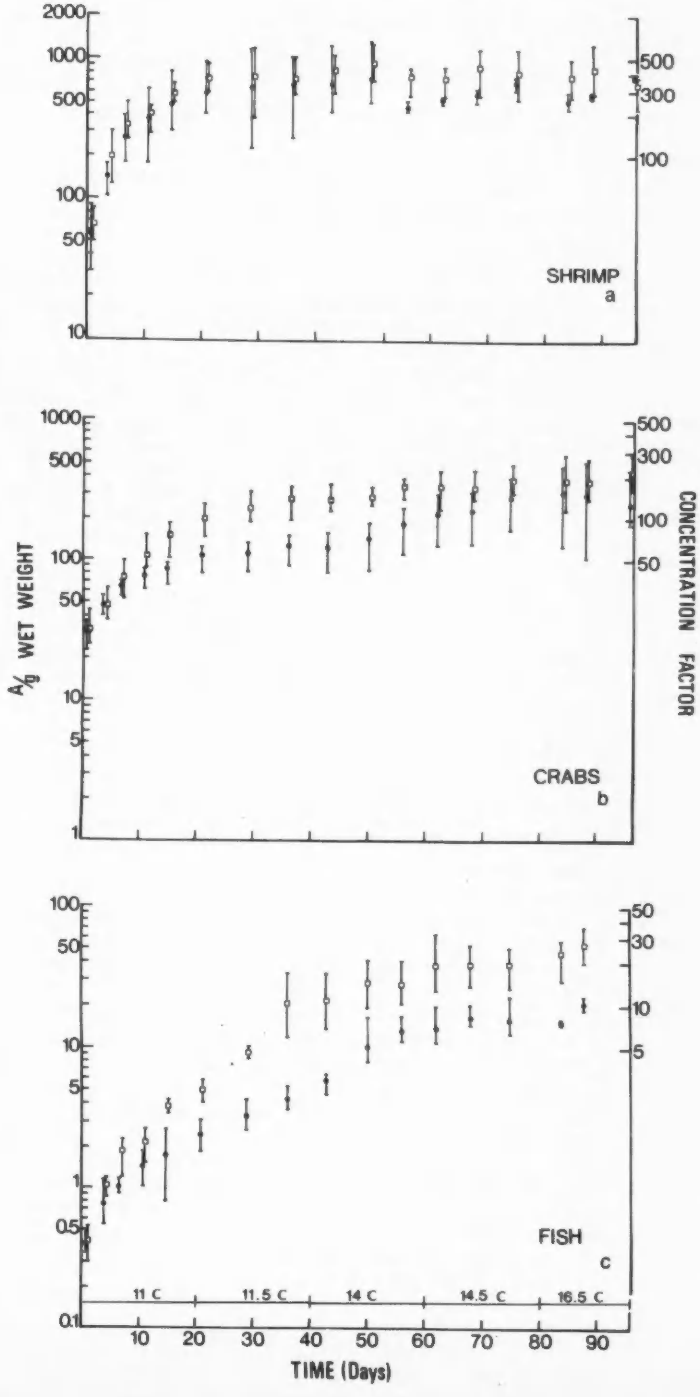

2000
1000
500
100
50
10
500
300
100
SHRIMP
a
1000
500
100
50
10
5
1
500
300
100
50
A/g WET WEIGHT
CONCENTRATION FACTOR
CRABS
b
100
50
10
5
1
0.5
0.1
50
30
10
5
FISH
c
11 C
11.5 C
14 C
14.5 C
16.5 C
10
20
30
40
50
60
70
80
90
TIME (Days)

TABLE 2. Stable zinc, ^{65}Zn, and specific activity in water samples from the experimental basin.

Day	μCi ^{65}Zn/liter	μg total Zn/liter	Specific activity (nCi ^{65}Zn/μg Zn)
0	3.18	23.3	136
96	2.30[a]	117.1	19.6

[a]Difference due to physical decay of isotope during the experiment.

TABLE 3. Mean whole-body concentration factors of ^{65}Zn (*CF) and stable zinc (CF) in experimental organisms. Radiozinc analyses were performed on remaining organisms sacrificed at the end of the accumulation period. Stable zinc measurements were made on all experimental animals and concentration factors were computed using the initial zinc concentration in the water. Numbers in parentheses indicate the number of individuals analyzed.

^{65}Zn uptake pathway	Shrimp		Crabs		Fish		Mussels	
	*CF	CF	*CF	CF	*CF	CF	*CF	CF
Water	380 (2)	2020 (6)	130 (4)	520 (6)	10 (4)	1400 (5)	170 (6)	580 (6)
Food and water	380 (4)	3200 (6)	210 (5)	450 (6)	25 (4)	900 (4)		

Considering the possibility that the system was contaminated with stable zinc late in the experiment, it was felt that the specific activity in the water on the first day probably most closely reflected that which the animals experienced during the major portion of the study. If comparisons are made between specific activities of animals (Table 1) and water (Table 2), it can be seen that isotopic equilibrium had not been reached after 96 days exposure, although in the case of shrimp, and possibly crabs, net ^{65}Zn accumulation appeared to cease or slow down before the termination of the experiment. An examination of relative differences between concentration factors based on radioisotope content and stable zinc measurements in the organisms and water leads to the same conclusion (Table 3).

Results of previous studies have also shown that concentration factors for ^{65}Zn and other radioisotopes in certain adult fish, shrimp, and mussels accumulating the radioisotope directly from water have fallen far short of those based on stable element data (Pentreath 1973a, b, c; Fowler and Benayoun 1974). In the case of shrimp and possibly crabs, even the frequent ingestion of relatively high ^{65}Zn concentrations in food 3 times a week failed to significantly increase the ^{65}Zn body burden over that reached by direct accumulation from water. These findings suggest that in adult individuals of the species studied, there exist zinc pools that exchange only very slowly, if at all, with zinc atoms absorbed from water or ingested with the organism's food. If this is indeed the case, then it is evident that only those individuals that have spent a significant portion of their actively growing life stages in a radioactive medium could achieve the same specific activity found in their surrounding environment. As has been pointed out by Bowen et al. (1971) and Lowman et al. (1971), this consideration would be especially important for organisms with long life cycles relative to the turnover time of the element in the organism.

Clearly, with certain adult crustaceans such as shrimp and crabs the food pathway for total zinc accumulation does not appear to be of such overriding importance as has been generally accepted. This result came as something of a surprise to us. Even in the case of adult fish, ^{65}Zn accumulation through the food pathway accounted for only 2.5 times more radioactivity than the level reached following direct accumulation from water after a 3-mo period in the contaminated ecosystem. It should be kept in mind that the choice of diet and the feeding regime in this study were strictly arbitrary. We hoped that diet and biomass ingested would closely reflect that encountered in the natural environment; nevertheless, fluctuations in feeding rates as well as changes in food quality normally experienced by these organisms might substantially alter zinc accumulation kinetics.

Acknowledgments

The International Laboratory of Marine Radioactivity operates under a tripartite agreement between the International Atomic Energy Agency, the Government of the Principality of Monaco, and the

Oceanographic Institute at Monaco. Support for the present work is gratefully acknowledged. We thank Dr F. Cross, Dr D. Wolfe, and Mr J. Willis for constructive criticisms.

Baptist, J. P., and C. W. Lewis. 1969. Transfer of ^{65}Zn and ^{51}Cr through an estuarine food chain, p. 420–430. *In* D. J. Nelson and F. C. Evans [ed.] Symposium on radioecology. Proc. second national symposium. USAEC Technical Information Extension, Oak Ridge, Tenn. 1971.

Bowen, V. T., J. S. Olson, C. L. Osterberg, and J. Ravera. 1971. Ecological interactions of marine radioactivity, p. 200–222. *In* Radioactivity in the marine environment. National Academy of Sciences, Washington, D.C.

Fowler, S. W., and G. Benayoun. 1974. Experimental studies on cadmium flux through marine biota, p. 159–178. *In* Comparative studies of food and environmental contamination. IAEA., Vienna.

Hoss, D. E. 1964. Accumulation of zinc-65 by flounder of the genus *Paralichthys*. Trans. Am. Fish. Soc. 93: 364–368.

Kameda, K., M. Shimizu, and Y. Hiyama. 1970. On the uptake of ^{65}Zn and concentration factor of Zn in marine organisms. II. Changes in Zn and ^{65}Zn concentration in rearing water. J. Radiat. Res. 11: 44–52.

Lowman, F. G., T. R. Rice, and F. A. Richards. 1971. Accumulation and redistribution of radionuclides by marine organisms, p. 161–199. *In* Radioactivity in the marine environment. National Academy of Sciences, Washington, D.C.

Pentreath, J. R. 1973a. The accumulation from water of ^{65}Zn, ^{54}Mn, ^{58}Co and ^{59}Fe by the mussel, *Mytilus edulis*. J. Mar. Biol. Assoc. U.K. 53: 127–143.

1973b. The roles of food and water in the accumulation of radionuclides by marine teleost and elasmobranch fish, p. 421–436. *In* Radioactive contamination of the marine environment. IAEA, Vienna.

1973c. The accumulation from seawater of ^{65}Zn, ^{54}Mn, ^{58}Co and ^{59}Fe by the thornback ray, *Raja clavata* L. J. Exp. Mar. Biol. Ecol. 12: 327–334.

Polikarpov, G. G. 1966. Radioecology of aquatic organisms. Reinhold Publishing Corporation, New York, N.Y. 314 p.

Migrations and Biological Characteristics of Atlantic Mackerel (*Scomber scombrus*) Occurring in Newfoundland Waters

J. A. MOORES, G. H. WINTERS, AND L. S. PARSONS

Department of the Environment, Fisheries and Marine Service,
Biological Station, St. John's, Nfld. A1C 1A1

MOORES, J. A., G. H. WINTERS, AND L. S. PARSONS. 1975. Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. J. Fish. Res. Board Can. 32: 1347–1357.

Mackerel migrate to Newfoundland waters from July to November and exhibit periodic fluctuations in abundance. Recent taggings have shown extensive migrations from Newfoundland to ICNAF Statistical Area 6. Various biological characteristics of mackerel from Newfoundland waters are reported and compared with those for mackerel caught in the New England area. A consideration of tagging results, biological characteristics, and ecological factors indicates that for assessment purposes mackerel inhabiting ICNAF Subareas 3–6 should be treated as one stock rather than assessed separately as northern and southern contingents each with a separate quota.

MOORES, J. A., G. H. WINTERS, AND L. S. PARSONS. 1975. Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters. J. Fish. Res. Board Can. 32: 1347–1357.

Le maquereau bleu émigre vers les eaux de Terre-Neuve de juillet à novembre et accuse des fluctuations périodiques d'abondance. Des marquages récents ont démontré des migrations d'envergure depuis Terre-Neuve jusque dans l'aire statistique 6 de l'ICNAF. Les auteurs mentionnent diverses caractéristiques biologiques du maquereau bleu des eaux de Terre-Neuve et les comparent avec celle du maquereau capturé dans la région de la Nouvelle-Angleterre. L'analyse des résultats du marquage, des caractères biologiques et des facteurs écologiques indique qu'aux fins de l'évaluation, le maquereau habitant les sous-aires 3–6 de l'ICNAF devrait être considéré comme un seul stock plutôt que deux, l'un septentrional et l'autre méridional, chacun avec un contingent de capture séparé.

Received September 16, 1974
Accepted April 21, 1975

Reçu le 16 septembre 1974
Accepté le 21 avril 1975

ATLANTIC mackerel (*Scomber scombrus*) are seasonal migrants to Newfoundland waters, appearing in abundance in July and disappearing again in October and November. Although reported from as far north as Black Island, Labrador (53°46′N) (Parsons 1970), the mackerel is basically a warmwater species and its abundance in Newfoundland waters has fluctuated in response to environmental conditions (Templeman 1966). The earliest landing records indicate that during the late 1800s there were two short periods of low abundance: 1870–72 and 1879–80 (Templeman 1966). After 1880 mackerel virtually disappeared from Newfoundland waters and did not become abundant again until the mid-1940s during a period of climatic warming. Landings declined considerably during the late 1950s, possibly due in part to the effects of a major fungus disease (Tibbo and Graham 1963). Recently mackerel have again appeared in abundance in Newfoundland waters with landings increasing from just over 300 metric tons in 1969 to nearly 1600 metric tons in 1972 (Table 1). The bulk of the landings has always been taken from coastal waters along eastern Newfoundland in ICNAF Divisions 3K and 3L (Fig. 1).

There is little published information on population characteristics of mackerel in Newfoundland waters. Most is related to distribution limits (Leim and Scott 1966; Parsons 1970) or the occurrence of mackerel eggs, larvae, and juveniles (Dannevig 1918; Sette 1943; Parsons and Hodder 1970). Parsons and Hodder (1970) reported the occurrence of at least sporadic mackerel spawning in the southern Newfoundland area. Tagging studies (Parsons and Moores 1974) and the patterns of landings (Anderson 1973) suggested that the recent rapid expansion in mackerel landings from ICNAF Subareas 5 and 6 (381,000 metric tons in 1973) may be based partially on the northern population of mackerel. This paper presents the results of an investigation of certain facets of the biology of mackerel in Newfoundland coastal

Printed in Canada (J3567)
Imprimé au Canada (J3567)

TABLE 1. Canadian Atlantic mackerel (*Scomber scombrus*) landings (metric tons) in ICNAF Subareas 2, 3, and 4, 1963–72.

Year	Subarea 2	Subarea 3	Subarea 4	Total	% total catch
1972		1579	20780	22359	73
1971	207	1299	22990	24496	60
1970	20	842	19097	19959	79
1969		314	17247	17561	75
1968		370	20449	20819	53
1967		54	11189	11243	99
1966		93	12728	12821	90
1965		187	11403	11590	97
1964		846	10114	10960	98
1963		373	6100	6473	98

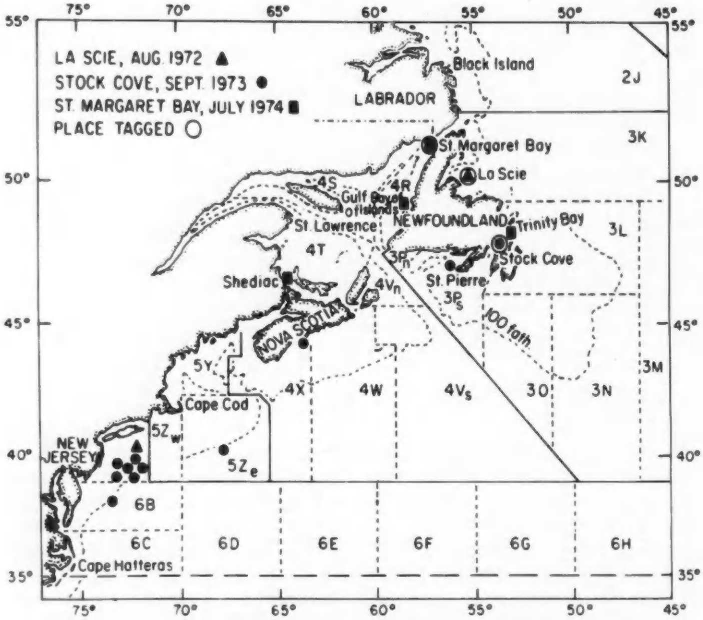

LA SCIE, AUG. 1972 ▲
STOCK COVE, SEPT. 1973 ●
ST. MARGARET BAY, JULY 1974 ■
PLACE TAGGED ○
Black Island
LABRADOR
2J
3K
St. Margaret Bay
La Scie
4S
4R
Gulf of St. Lawrence
Bay of Islands
NEWFOUNDLAND
Trinity Bay
3L
4T
3Pn
Stock Cove
St. Pierre
Shediac
4Vn
3Ps
100 fath
NOVA SCOTIA
5Y
4X
4W
4Vs
3O
3N
3M
Cape Cod
5Zw
5Ze
NEW JERSEY
6B
6C
6D
6E
6F
6G
6H
Cape Hatteras
75°
70°
65°
60°
55°
50°
45°
40°
35°

FIG. 1. ICNAF Subareas 2–6 with results of tagging studies.

waters, based on biological sampling of commercial landings and tagging studies.

Materials and Methods

Random samples of mackerel from nonselective gears (purse seines, ring nets, herring traps) were obtained from fishermen or from processing plants and were examined fresh or after being frozen for a period of several weeks. Data were obtained on total length, whole weight, sex, maturity, gonad weight, degree of stomach fullness, and otoliths were removed for age determination.

Total lengths were measured to the nearest millimeter from the tip of the lower jaw to the end of the longest caudal lobe directed posteriorly in line with the body. Whole weight and gonad weight were determined to the nearest gram. No significant difference ($P > .05$) was found between the lengths and weights of fish sampled fresh and those sampled after freezing and thawing.

The stage of maturity was determined by gross examination of the gonads. Numerical values for each stage were designated according to the maturity scale adopted by ICNAF (Anon. 1964) for herring. The degree of stomach fullness was estimated on a five-point scale: 0 = empty, 1 = ¼ full, 2 = ½ full, 3 = ¾ full, and 4 = full.

TABLE 2. Mackerel taggings in Newfoundland with dates and areas of recapture.

Place tagged	Date tagged	No. tagged	Date of recapture	Place of recapture
La Scie	Aug. 30, 1972	1450	Sept. 1–25, 1972	5 tags La Scie area
			Dec. 28, 1972	40°05′N, 72°27′W(6A)
Stock Cove	Sept. 7–8, 1973	9000	Sept. 9–30, 1973	54 tags Trinity Bay area
			Oct. 30, 1973	St. Pierre (3Ps)
			Jan. 12, 1974	39°46′N, 72°37′W(6A)
			Jan. 25, 1974	39°20′N, 73°31′W(6A)
			Feb. 2, 1974	39°37′N, 72°06′W(6A)
			Feb. 15, 1974	39°46′N, 72°27′W(6A)
			Feb. 1974	(6A)
			Mar. 3, 1974	38°27′N, 73°23′W(6B)
			Mar. 30, 1974	40°23′N, 68°04′W(5Ze)
			Apr. 15, 1974	39°20′N, 72°44′W(6A)
			June 12, 1974	Indian Hr., N.S. (4X)
St. Margaret's Bay	July 27–31, 1974	6000	Sept. 16, 1974	Bay of Islands, Nfld.
			Sept. 29, 1974	Shediac, N.B. (4T)
			Sept. 1974	2 tags Trinity Bay, Nfld.

Ages were determined from otoliths placed whole into depressions in a black plexiglass tray according to the method of Watson (1965). The otoliths were immersed in 95% ethanol and read under reflected light. Otoliths were aged independently by two experienced readers with disagreements being resolved by a third reader or by mutual agreement. An arbitrary birth date of January 1 was assigned and ages were transformed into age-groups. Thus, fish having one completed summer zone on the otolith and caught before January 1 were assigned to the 0 age-group while fish caught after January 1 with one complete summer zone were assigned to age-group 1. All fish older than age 10 were classed as 10+ yr of age.

Mackerel for tagging were captured in bar seines and herring traps operated by commercial fishermen. A small-meshed holding pound, 5 m deep and supported on the surface by two diagonally secured 6-m poles, was attached to the head rope of the seine or trap and mackerel were transferred to the pound by depressing the headrope and allowing the mackerel to swim over. The actual tagging operation was conducted in small boats equipped with plastic tagging tanks capable of holding 25–50 live mackerel. Mackerel were transferred from the holding pound to the tagging tanks with a dipnet.

Two types of external tags were used — the FD-68 Anchor tag and the FT-2 Dart tag both made of #20 vinyl tubing approximately 64 mm (2½ inches) long. The FD-68 Anchor tag was applied with a tagging gun described by Dell (1968); the FT-2 Dart tag was applied with sharp-pointed hollow stainless steel applicators. Both types of tags were inserted in the dorsal region just posterior to and below the second dorsal fin.

Results

TAGGING

Three mackerel tagging experiments were carried out in the Newfoundland area during 1972–74 (Table 2). In 1972, 1450 mackerel were tagged in LaScie on August 30 (Fig. 1); 9000 mackerel were tagged in Stock Cove, Trinity Bay, on September 6–7, 1973; and 6000 mackerel were tagged in St. Margaret's Bay from July 27 to August 1, 1974.

The returns from these taggings have shown both local and long distance migrations (Table 2, Fig. 1). Six recaptures were reported from the LaScie tagging (Parsons and Moores 1974); five were from the LaScie area while the sixth was returned from ICNAF Statistical Area 6A. A total of 64 fish were recaptured from the Stock Cove tagging, 54 of which were recaptured in Trinity Bay. Of the other 10 tags, one was recaptured off St. Pierre et Miquelon in October 1973; six were recaptured in ICNAF statistical Area 6A from January to April 1974; one was recaptured in Statistical Area 6B in February; one was recaptured in Subdivision 5Ze in March; and one was recaptured off Halifax, N.S., in June. Early returns from the St. Margaret's Bay (Fig. 1) tagging show one recapture from the Bay of Islands (Fig. 1), one from Shediac, New Brunswick, and two from Trinity Bay.

The tagging results suggest that the mackerel that appear in Newfoundland waters migrate extensively. There is movement of mackerel from the west coast of Newfoundland southwards to the Gulf of St. Lawrence and eastwards to the east coast of Newfoundland via the Strait of Belle Isle. The results from the 1973 tagging confirm the long-distance migration of mackerel from the east coast of Newfoundland southward during the fall to overwintering grounds off the New England coast where they are subjected to exploitation by the international fleet. The pattern of the returns suggests that a return migration occurs during May–June.

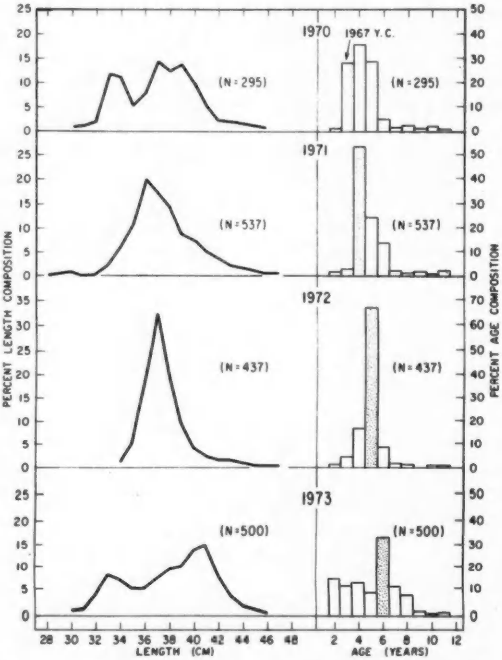


FIG. 2. Length and age compositions of mackerel caught in Newfoundland coastal waters, 1970–73.

LENGTH AND AGE COMPOSITION

Data from commercial catches by nonselective gears in Newfoundland waters (Fig. 2) indicate that the 1967 year-class has dominated from 1971 onwards and also contributed very significantly to catches in 1970. The percentage contribution of this year-class peaked at about 66% in 1972 and fell to 33% in 1973. The 1966 year-class that was dominant at 35% in 1970 fell to 24% in 1971 and to less than 11% in 1973. The 1968–70 year-classes appear to be fairly weak, each year-class contributing less than 13% to the catches in 1973. The 1971 year-class comprised 14% of those sampled in 1973 as 2-yr-olds and would appear to be somewhat stronger than most recent year-classes. The peaks in length frequencies (Fig. 2) reflect the size composition of the dominant year-classes with total lengths ranging from 28 to 47 cm. Old fish (>8 yr old) have not formed a significant percentage of the fish examined and by 1970 the 1959 year-class, reported by MacKay (1967, 1973) as being very strong, had nearly disappeared from the catches.

MATURITY COMPOSITION

Table 3 indicates that from 1970–73 there was a consistent appearance of mackerel in spawning stages (4–6) in the Newfoundland area. Most of the mackerel examined in June were in spawning condition, whereas the percentage of ripe fish in July fluctuated from 89% in 1972 to just over 18% in 1973 and nil during 1971. With the exception of 1972, fish in spawning condition were not present in the samples after July when spent fish and those recovering dominated the catches. Most of the ripening mackerel were from samples obtained from southeastern Newfoundland (ICNAF Subdivision 3Ps) and Conception Bay (3L). Farther north along the east coast of Newfoundland and particularly in Labrador, mackerel tended to appear later in the summer (usually late July–early August) and were mainly comprised of spent and recovering fish, as was reported by Parsons and Hodder (1970). Immature fish were not present in the catches in June but tended to increase in percentage contribution from July to August. This pattern is similar to that reported by MacKay (1973) for mackerel in the Nova Scotia area.

Comparison of age compositions and mean ages of ripe and spent mackerel caught in southeastern Newfoundland during 1970–73 (Table 4) suggests that the older (and hence larger) fish spawn first. A similar pattern was observed in the southern Gulf of St. Lawrence (4T) mackerel population (MacKay 1967).

GROWTH

Average lengths-at-age of mackerel sampled in Newfoundland coastal waters during June–July and August for the years 1970–73 are shown in Table 5. There is a slight decrease in mean length-at-age from the June–July period to August both by year-class and by age. This reflects the general trend of larger and older fish spawning first (Table 4) and also the influx of immature fish in July and August (Table 3). Comparison of the mean length of the various year-classes at each age suggests that the dominant 1967 year-class is neither consistently longer nor shorter than adjacent year-classes. These data do not therefore support the inverse relationship between growth rate and year-class size reported by MacKay (1973) for the 1959 and 1967 year-classes of mackerel in the southern Gulf of St. Lawrence.

The growth curve of mackerel in the Newfoundland area was analyzed by the von Bertalanffy (1938) growth equation according to the

Table 3. Maturity composition by month of mackerel caught in the Newfoundland area from 1970–73.

		% at each maturity stage				
Year	Month	Stages 1–2 (immature)	Stage 3 (maturing)	Stages 4–6 (ripening)	Stages 7–8 (recovering spent)	No. examined
1970	June					
	July	1.5	10.5	68.0	20.0	200
	Aug.	20.0	5.7		74.3	35
	Sept.	19.4			80.6	62
1971	June	0.6	8.4	80.1	10.9	311
	July	12.2	4.9		82.9	123
	Aug.	4.0			96.0	99
	Sept.					
1972	June		6.0	94.0		50
	July		3.0	89.0	8.0	100
	Aug.	3.0		3.0	94.0	100
	Sept.	2.6			97.4	189
1973	June					
	July	10.8	27.0	18.2	44.0	148
	Aug.	22.0	4.0		74.0	50
	Sept.	22.3			77.7	300

Table 4. Age composition of ripe and spent mackerel caught in the Newfoundland area during June–July, 1970–73.

	% at age												
Maturity condition	1	2	3	4	5	6	7	8	9	10	10+	No. examined	Mean age
Ripe		0.5	8.7	46.8	23.7	13.1	3.6	1.5	1.0	0.8	0.3	389	4.69
Spent			1.6	35.2	17.2	29.5	7.4	6.6	0.8	0.8	0.8	122	5.37

method of Allen (1966). Since all of the lengths were obtained during the June–August period, July was taken as the midpoint of the time interval and ages were defined as fractions of a year, e.g. age 2.6, 3.6, etc. The resulting von Bertalanffy growth curve (Fig. 3) was $L_t = 42.9\ (1–e^{-0.36(t+1.14)})$. Values calculated by the fitted curve agree with the observed points.

A comparison of growth data of mackerel from various areas is provided in Table 6. Allocation of growth data to specific areas in ICNAF Subarea 5 and Statistical Area 6 was not possible because of the lack of information on sampling details in the original sources. Where lengths have not been defined (Isakov 1973; Anon. 1973) it has been assumed that they refer to fork lengths and consequently they have been converted to total lengths using the appropriate conversion factor (Anderson 1973). Table 6 suggests that the mackerel sampled in Subarea 5 and Statistical Area 6 during the winter period are similar in size-at-age to the mackerel population sampled during the summer months in Subarea 4 (Stobo and Hunt 1974) and the Newfoundland area. The inconsistent variation in size-at-age in the older age-groups is probably due to errors in age determination rather than real differences in growth.

Analysis of length–weight data (Fig. 4) indicates that weight increases with length at a rate slightly faster than expected from the Cube Law. The recovery in body condition after spawning is indicated by the greater weight-at-length of mackerel sampled in September relative to the June–July period.

AGE AND LENGTH AT MATURITY

Analyses of maturity stage data indicate that mackerel caught in the Newfoundland area mature between ages 2 and 4 (Table 7). Females tend to mature at a slightly faster rate than males but both sexes contain only a few immature individuals at age 4 and are 100% mature at age 5.

TABLE 5. Mean length-at-age of mackerel from the Newfoundland area for the period June–July (A) and August (B) 1970–73. No. of fish examined in brackets.

Year	1	2	3	4	5	6	7	8	9	10	10+
(A) June–July 1970–73											
1970	—	—	35.4(18)	37.9(80)	38.7(73)	40.9(13)	43.7(3)	43.0(4)	45.0(1)	43.3(4)	—
1971	—	31.0(8)	35.3(7)	36.1(218)	38.4(113)	39.4(68)	41.2(6)	42.0(1)	43.5(4)	43.0(2)	43.7(10)
1972	—	—	36.0(2)	38.4(11)	38.8(71)	41.2(30)	41.9(16)	43.5(4)	44.3(6)	45.0(2)	44.6(8)
1973	—	32.0(14)	35.0(7)	36.6(18)	39.0(11)	40.3(58)	40.6(19)	41.6(14)	43.8(4)	43.0(1)	45.0(4)
Years combined	—	31.6(22)	35.3(34)	36.6(327)	38.6(268)	40.1(169)	41.4(44)	42.2(23)	44.0(15)	43.6(9)	44.3(22)
(B) August 1970–73											
1970	—	33.0(1)	32.9(24)	36.7(6)	37.0(4)	—	—	43.0(1)	—	—	44.0(1)
1971	—	—	36.2(6)	36.2(66)	37.1(16)	43.8(4)	41.0(2)	42.0(1)	44.5(2)	42.0(1)	43.0(2)
1972	—	—	36.8(4)	37.9(14)	38.3(50)	39.4(25)	40.4(5)	40.0(1)	43.0(1)	—	—
1973	—	32.3(11)	35.0(6)	36.7(6)	38.3(4)	39.2(17)	39.0(5)	43.0(1)	—	—	—
Years combined	—	32.4(12)	34.1(40)	36.5(92)	38.0(74)	39.7(46)	39.9(12)	42.0(4)	44.0(3)	42.0(1)	43.3(3)

TABLE 6. Comparison of mean length of mackerel from various areas.

Age	Newfoundland Calculated (Jan.)	Newfoundland Observed (July)	Subarea 4 (calculated Jan.)[a]	New England (Jan.–Feb.)[b] (observed)	New England (Jan.–Feb.)[c] (observed)
1	231		222	232	217
2	291	318	275	284	272
3	333	363	315	341	325
4	362	374	345	353	356
5	382	389	369	366	381
6	397	399	387	374	405
7	406	413	400	402	415
8	413	421	411	424	
9	418	438	419	435	
10	421	430	425		

[a] Stobo and Hunt 1974.
[b] ICNAF Redbook, 1973, Part 1, p. 94.
[c] Isakov 1973.

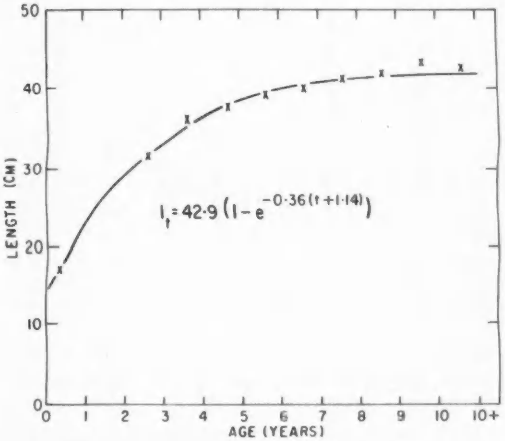


FIG. 3. Fitted von Bertalanffy growth curve of mackerel from Newfoundland waters. (x — observed mean lengths).

Although no age 1 fish were present in the samples used in these analyses, a few have been caught by small-meshed gillnets and all have been immature. The smallest mature mackerel caught in the Newfoundland area was 32 cm and the largest immature fish was 37 cm (Fig. 5). The 50% maturity point was 339 mm for females and 347 mm for males with the average length being 343 mm. Since this mean length is based on fish sampled in June–September, the mean length of maturity at the beginning of the year (January) is probably in the range of 30–31 cm.

SEX RATIO

During the period 1970–73 there has been a significant fluctuation in the sex ratio of mackerel in the Newfoundland area (Table 8). Females tend to be predominant in mature fish, whereas in the immature stages males have predominated. In 1973 when 90 immatures were sampled, the sex ratio was close to 1:1. For both matures and immatures combined the ratio of males to females for the years sampled was 1.00:1.25. MacKay (1967) also found proportionally more females in his samples but only slightly so with a ratio of 1 male to 1.06 females. Steven (1952) found a ratio of 1 male to 1.07 females in mackerel from the English Channel and Celtic Sea.

The more rapid maturation rate of female mackerel relative to males, particularly in the

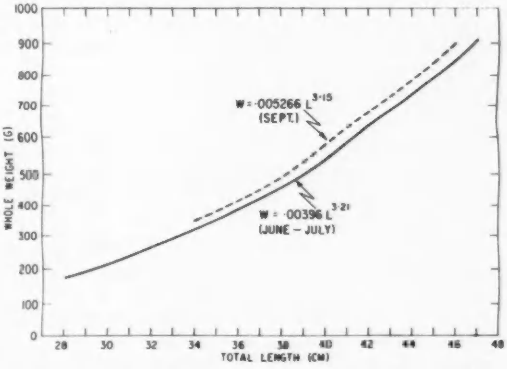


FIG. 4. Length–weight curves of mackerel samples during June–July and September.

TABLE 7. Number of mackerel examined and percentage mature by age from Newfoundland waters, 1970–73.

	Females		Males		Combined	
Age	No.	%	No.	%	No.	%
2	51	31.4	41	9.8	92	22.8
3	112	93.8	72	73.6	184	85.9
4	305	96.7	257	91.8	562	94.1
5	356	100.0	305	100.0	661	100.0
6+	309	100.0	225	100.0	534	100.0

TABLE 8. Sex ratio of mackerel obtained from commercial gears in Newfoundland 1970–73.

	Immature		Mature		Imm. + Mat.	
Year	No.	% ♀	No.	% ♀	No.	% ♀
1970	14	28.6	226	71.2	240	68.8
1971	20	20.0	498	60.2	518	58.7
1972	14	0.0	773	50.8	787	49.9
1973	90	48.9	408	55.6	498	54.4
Total	138	37.7	1905	56.7	2043	55.5

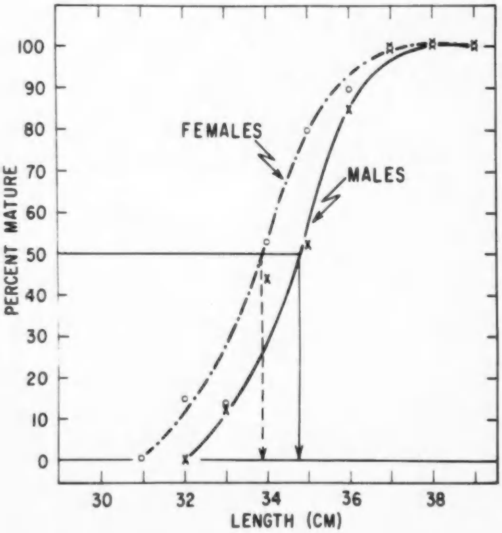


FIG. 5. Maturation ogives of male and female mackerel caught in the Newfoundland area.

younger age-groups could account for the predominance of females in mature fish. If one assumes that mortality is not sex specific, then the convergence of the maturity curves of males and females with age implies that the proportion of males as mature fish will increase steadily to age 5 when 100% maturity is reached for both sexes. If the stock is dominated by a strong year-class such as the 1967 year-class, then the sex ratio of the stock as a whole will reflect this pattern. This, therefore, may explain the declining predominance of mature females from 1970 to 1972 as the 1967 year-class became fully mature at age 5 in 1972. Similarly, in 1973 the relative strong 1971 year-class at age 2 contained a relatively higher proportion of mature females than males.

FEEDING HABITS

An analysis of the degree of stomach fullness (Fig. 6) shows that most mackerel sampled had little or no food in their stomachs. The most extensive feeding was observed during the month of July when only 36% of the stomachs examined were empty and 16% were full. October shows the least observed feeding with 95% of the stomachs examined being empty. June and August show feeding to a limited degree with June having 73% empty and 7% full stomachs, while August has 77% empty and 1% full.

A limited number of stomachs (155) was examined in greater detail (Table 9). During the summer months, June–August, mackerel feed predominantly on capelin which are plentiful in inshore waters at this time. Planktonic organisms, primarily euphausiids, are the main food item

TABLE 9. Percent occurrence of food items in mackerel stomachs.

Food item	% occurrence					
	June	July	Aug.	Sept.	Oct.	Total
Capelin	74	81	52			66
Fish remains	13	16	26		17	15
Euphausiids		2		100	66	12
Hyperiids			22			3
Decapod larvae	13					2
Copepods		1				1
Gastropod larvae					1	1

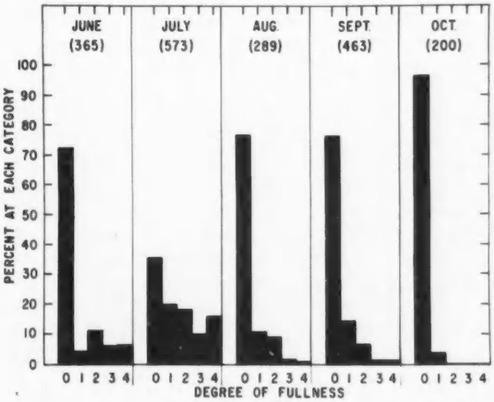


FIG. 6. Degree of fullness of mackerel stomachs collected from specimens caught in Newfoundland coastal waters.

during September–October. From this limited analysis it would appear that mackerel are opportunistic feeders that consume planktonic organisms, but also consume larger food items, such as capelin, whenever they are available.

Discussion

The existence of two major spawning areas for mackerel, one in the Bight between New Jersey and Long Island (ICNAF Divisions 6A and 5Z) and the other in the southern Gulf of St. Lawrence (ICNAF Division 4T), together with the availability of mackerel in both the southern (Gulf of Maine) and northern (Gulf of St. Lawrence) areas during the summer support Sette's (1950) hypothesis of two mackerel stocks in the northwest Atlantic. In spite of the wide separation of spawning areas, no significant differences in the meristic and biochemical characteristics of the two contingents have been found (Sette 1950; MacKay 1967). Sette (1950) stated that there may be mixing between the two mackerel contingents during the overwintering period, although the main area occupied by the northern contingent was probably north of that occupied by the southern contingent. The degree of mixing that occurs, however, has not been quantified. Recently the international fishery, which occurs in ICNAF Divisions 6A and 5Z, has been considered to be exploiting only the southern contingent, and stock assessments have been performed for this fishery without assessing the degree of intermixing (Anon. 1973).

Tagging studies reported here show that mackerel from the Newfoundland area have contributed to the international mackerel fishery off New England during the winter. During the same period and in the same general locality the international fleet recaptured 20 mackerel tagged by the St. Andrews Biological Station off southwest Nova Scotia during the fall of 1973 (W. T. Stobo personal communication). During the period 1925–28 nearly 8000 mackerel were tagged during the summer period (mainly June) along southwest Nova Scotia (Sette 1950), 35 of which were recaptured during the fall–spring period from United States waters, mainly in the Cape Cod–New Jersey area (ICNAF Divisions 5Z and 6A). During the same period 8500 mackerel were tagged in United States waters with only one recapture being recorded in Canadian waters. This single capture was from a release of mixed fish containing both northern and southern contingent mackerel (Sette 1950). These results indicate that mackerel from as far north as Division 3K mix with those from Subarea 4 in a common overwintering area off the New England coast.

The existence of a southern overwintering area for mackerel is indeed to be expected from the temperature requirements of the species. Sette (1950) reports observational evidence that suggests that mackerel prefer temperatures above 8 C, although temperatures down to 7 C are frequently tolerated; they are only rarely found

TABLE 10. Percent total catch, 1969–72, by month for divisions in Subareas 5 and 6 and Subareas 5 and 6 combined. (The combined percentage includes catches not allotted to specific divisions.)

Month	5Ze	5Zw	6A	6B	6C	% catch for SA5+6
Jan.	1.2	2.2	6.6	1.6	1.0	12.5
Feb.	0.9	0.3	3.5	2.7	1.8	9.2
Mar.	1.0	1.1	5.5	5.2	3.8	16.5
Apr.	2.0	1.4	4.8	6.8	0.4	15.7
May	5.3	3.0	0.3	0.1	—	12.4
June	3.2	2.4	0.2	—	—	6.3
July	2.9	0.8	—	—	—	4.1
Aug.	2.8	0.5	—	—	—	3.6
Sept.	1.9	0.2	—	—	—	2.3
Oct.	1.6	0.7	0.1	—	—	2.4
Nov.	3.1	0.5	0.5	—	—	4.4
Dec.	4.9	0.7	4.6	—	—	10.6

in temperatures as low as 4 or 5 C. From the hydrography of the Scotian Shelf (Hachey 1953; McLellan 1954a, b; McCracken 1965), it appears that winter temperature conditions on the Scotian Shelf, with the exception of the Scotian Gulf where bottom temperatures are in the lower range of preferred temperature, are not favorable for overwintering concentrations of mackerel. This does not, however, exclude the possibility of schools overwintering in slope water on the oceanic side of the Scotian Shelf. Nevertheless, mackerel catches on the Scotian Shelf during the December–April period have been extremely low despite the fact that the area is traversed frequently by vessels with suitable gear for catching mackerel.

The pattern of mackerel landings in Subareas 5 and 6 (Table 10) supports the general migration pattern of northern mackerel as suggested by tag recaptures. The migratory pattern based on catch data suggests that there is an influx of mackerel into Subdivision 5Ze during November. During December mackerel apparently continue to move through division 5Ze and into Division 6A. From January to April the bulk of the mackerel are caught in Divisions 6A and 6B. In May and June the mackerel apparently move north from 6B through 6A and 5Ze. The catches show a marked decline from June to October as the northern contingent presumably moves out of the New England area.

In summary, tagging studies both recent and historical, similarities in growth, seasonal patterns of fishing activity and also ecological considerations suggest strongly that a large proportion of the so-called northern contingent of mackerel migrate southwards during the fall to overwinter in the offing of New England where they are exploited with the southern contingent in a mixed fishery. The relative contribution of each contingent to the international fishery is not known, but crude estimates of biomass levels of mackerel in the southern Gulf of St. Lawrence from population fecundity studies (MacKay 1973) suggest that the northern contingent is large. The so-called northern population of mackerel contributes at least partially and perhaps substantially to the international winter fishery in ICNAF Subareas 5 and 6. In the absence of precise information on the relative contribution of each contingent to this fishery, it would be prudent to incorporate all fisheries for mackerel in Subareas 3–6 into a single assessment.

Acknowledgments

We wish to thank the staff of the Pelagic Fish section of the St. John's Biological Station who assisted in the collection and examination of specimens and particularly Messrs C. I. Barbour, R. Chaulk, and M. F. Dawson who read the ages. We also wish to thank the many fishermen and fish plant operators who assisted us in our tagging programs and supplied us with samples.

ALLEN, K. R. 1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23: 163–179.

ANDERSON, E. D. 1973. Assessment of Atlantic mackerel in ICNAF subarea 5 and statistical area 6. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/14 Ser. No. 2916.

ANON. 1964. Report of standing committee on research and statistics. Append. I. Report of ad hoc group on herring and other pelagic fish. Int. Comm. Northwest Atl. Fish. Redbook Part I: 23–30.

1973. Report of ad hoc mackerel working group. Int. Comm. Northwest Atl. Fish. Redbook Part I: 87–94.

Dannevig, A. 1918. Biology of Atlantic waters of Canada. Canadian fish-eggs and larvae. Can. Fish. Exped. 1914–15: 74 p.

Dell, M. B. 1968. A new fish tag and rapid, cartridge fed applicator. Trans. Am. Fish. Soc. 97: 57–59.

Hachey, H. B. 1953. A winter incursion of slope water on the Scotian Shelf. J. Fish. Res. Board Can. 10: 148–153.

Isakov, V. I. 1973. Growth and total mortality of mackerel from the New England area. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/23 Ser. No. 2956.

Leim, A. H., and W. B. Scott. 1966. Fishes of the Atlantic coast of Canada. Bull. Fish. Res. Board Can. 155: 485 p.

MacKay, K. T. 1967. An ecological study of mackerel, *Scomber scombrus*, in the coastal waters of Canada. Fish. Res. Board Can. Tech. Rep. 31: 127 p.

1973. Aspects of the biology of Atlantic mackerel in ICNAF Subarea 4. Int. Comm. Northwest Atl. Fish. Res. Doc. 73/70 Ser. No. 3019.

McCracken, F. D. 1965. Distribution of haddock off the eastern Canadian mainland in relation to bottom temperature. Int. Comm. Northwest Atl. Fish. Spec. Publ. 6: 113–129.

McLellan, H. J. 1954a. Bottom temperatures on the Scotian Shelf. J. Fish. Res. Board Can. 11: 404–418.

1954b. Temperature-salinity relations and mixing on the Scotian Shelf. J. Fish. Res. Board Can. 11: 419–430.

Parsons, L. S. 1970. Northern range extension of the Atlantic mackerel, *Scomber scombrus*, to Black Island, Labrador. J. Fish. Res. Board Can. 27: 610–613.

Parsons, L. S., and V. M. Hodder. 1970. Occurrence of juvenile and spawning Atlantic mackerel in southeastern Newfoundland coastal waters. J. Fish. Res. Board Can. 27: 2097–2100.

Parsons, L. S., and J. A. Moores. 1974. Long-distance migration of an Atlantic mackerel, *Scomber scombrus*, tagged in Newfoundland waters. J. Fish. Res. Board Can. 31: 1521–1522.

Postuma, K. H. 1972. On the abundance of mackerel *Scomber scombrus* in the northern and northeastern North Sea in the period 1959–69. J. Cons. Cons. Int. Explor. Mer 34 (3): 445–465.

Sette, O. E. 1943. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 1. Early life history including growth, drift and mortality of the egg and larval populations. U.S. Fish Wildl. Serv. Fish. Bull. 50 (38): 149–237.

1950. Biology of the Atlantic mackerel (*Scomber scombrus*) of North America. Part 2. Migrations and habits. U.S. Fish Wildl. Serv. Fish. Bull. 51 (49): 251–358.

Steven, G. A. 1952. Contributions to the biology of the mackerel *Scomber scombrus* L. III. Age and growth. J. Mar. Biol. Assoc. U.K. 30: 549–568.

Stobo, W. T., and J. J. Hunt. 1974. Mackerel biology and history of the fishery in Subarea 4. Int. Comm. Northwest Atl. Fish. Res. Doc. 74/9 Ser. No. 3155.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. 154: 170 p.

Tibbo, S. N., and T. R. Graham. 1963. Biological changes in herring stocks following an epizootic. J. Fish. Res. Board Can. 20: 435–447.

von Bertalanffy, L. 1938. A quantitative theory of organic growth. Hum. Biol. 10: 181–213.

Watson, J. E. 1965. A tecnhique for mounting and storing herring otoliths. Trans. Am. Fish. Soc. 94: 267–268.

Movement, Growth, and Survival in a Stream Population of Wild Brook Trout (*Salvelinus fontinalis*) During a Period of Removal of Non-Trout Species

WILLIAM A. FLICK AND DWIGHT A. WEBSTER

Department of Natural Resources, N.Y. State College of Agriculture and Life Sciences, Cornell University, Ithaca, N.Y. 14853, USA

FLICK, W. A., AND D. A. WEBSTER. 1975. Movement, growth, and survival in a stream population of wild brook trout (*Salvelinus fontinalis*) during a period of removal of non-trout species. J. Fish. Res. Board Can. 32:1359–1367.

No well-defined changes in growth and survival rates of native brook trout (*Salvelinus fontinalis*) were detected during a 13-yr period when non-trout species were removed from a small Adirondack Mountain stream using fixed traps located throughout the system. The catch of non-trout species was about 124,000 weighing 2000 kg, and of trout, 13,000, weighing 500 kg. Slow growth characterized the population through this time, with mean lengths of 13.2, 17.3, and 21.3 cm at ages I+, II+, and III+, respectively. The weighted annual survival rate for ages II–V was 18%, with most deaths due to natural causes. The most striking observation was virtual cessation of movement of both trout and non-trout species after 7 yr, suggesting that the removal program had an effect on population behavior, even if it was not reflected in an improvement in trout growth.

FLICK, W. A., AND D. A. WEBSTER. 1975. Movement, growth, and survival in a stream population of wild brook trout (*Salvelinus fontinalis*) during a period of removal of non-trout species. J. Fish. Res. Board Can. 32: 1359–1367.

Les ombles de fontaine (*Salvelinus fontinalis*) sauvages indigènes de l'émissaire de l'étang Long croissent lentement, atteignant des longueurs d'environ 13.2, 17.3 et 21.3 cm aux âges I+, II+ et III+ respectivement. Le taux de survie annuel pondéré pour les âges de II à V est de 18%, la plupart des mortalités étant dues à des causes naturelles. Nous n'avons détecté aucun changement bien défini dans ces paramètres durant une période de 13 ans au cours de laquelle les espèces autres que l'omble de fontaine furent enlevées au moyen de trappes fixes placées dans tout le réseau du cours d'eau. Les déplacements des ombles de fontaine, aussi bien que ceux des autres espèces cessèrent presque complètement après 7 ans, ce qui donne à croire que le programme d'enlèvement eut, sur la population de poissons, un effet qui ne se refléta pas dans une amélioration de la croissance de l'omble de fontaine.

Received December 16, 1971
Accepted May 2, 1975

Reçu le 16 décembre 1971
Accepté le 2 mai 1975

DIMINUTIVE size is one of the striking characteristics of brook trout (*Salvelinus fontinalis*) inhabiting small infertile upland streams in the Adirondack Mountains of New York, USA. In Long Pond Outlet, the study stream, the average size of fish caught by angling is about 15 cm and specimens above 25 cm are rare. Although Adirondack waters are typically of low basic productivity, other factors such as competition must be considered as influencing growth rate.

The work on Long Pond Outlet began as a management project with the immediate objective of increasing the size of the trout by removal of non-trout and presumably, competitive, species. It was anticipated that data collected in the initial year or two would suffice as a comparative base for detecting major changes in growth and survival of trout. Cursory observations by the property owners over the 10 yr prior to the study indicated the trout were consistently small. The drastic change in movement pattern of trout that took place during removal of non-trout species was unexpected and interpretation of these data would have been enhanced by pretreatment observations. Nonetheless, these changes took place over several years and were consistent at two trapping stations so that some cause-and-effect relationships may not be an excessively presumptuous conclusion.

Description of Study Area

Long Pond Outlet is in the northern Adirondacks near Paul Smiths, New York State (Town of Waverly, Franklin County), at longitude 74° 31′, latitude 44° 27′ (Fig. 1). Local terrain is mostly of low relief at elevations of 460–550 m consisting of sand plains,

Printed in Canada (J2371)
Imprimé au Canada (J2371)

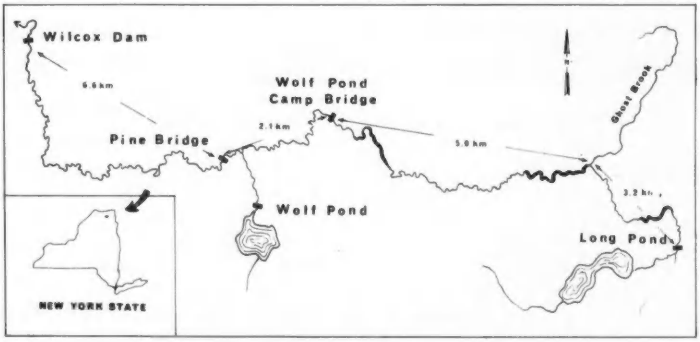


FIG. 1. Long Pond Outlet system showing location of fish traps.

moraine and extensive bogs and swamps. The stream is on privately owned Brandon Park and the section under consideration here has a watershed of 4300 ha extending from the headwaters downstream approximately 19 km. The study area, extending from Long Pond Dam to Wilcox, averaged about 7.6 m in width, with a total estimated main stream area of 12 ha. Two shallow headwater ponds, Long (17.8 ha) and Wolf (10.9 ha), were reclaimed for the first time, using rotenone, in 1951 and 1953, respectively. After leaving Brandon Park, Long Pond Outlet flows northward to join the West Branch of the St. Regis River, a tributary to the St. Lawrence River.

The stream has a low gradient (1.1 m/km), and meanders through dense alder thickets except for three stillwaters and five short rapids. This type of habitat is prone to beaver activity, but effects were kept to a minimum by systematic trapping. The water is stained brown due to drainage from extensive sphagnum, black spruce, and tamarack bogs. The watershed is relatively flat and has been extensively lumbered for the native white pine, but with upland regrowth in mixed hardwoods. Midsummer flow in the lower sections averaged approximately 0.4 m/s. Water temperatures commonly peaked above 20 C during midsummer, but dropped below 15 C at night. The stream is relatively unproductive and much of the bottom consists of sand, with the fluviatile forms of *Sparganium* and *Ceratophyllum* the major rooted aquatic plants.

Indigenous fish in the stream commonly taken in the traps consisted of brook trout, white sucker (*Catostomus commersoni*), common shiner (*Notropis cornutus*), creek chub (*Semotilus atromaculatus*), pearl dace (*Semotilus margarita*), cutlips minnow (*Exoglossum maxillingua*), and longnose dace (*Rhinichthys cataractae*).

A fish barrier dam was constructed in 1940 at Wilcox Rapids to block upstream movement of yellow perch (*Perca flavescens*). This was located near the lower boundary of the study area. At some time prior to 1953, the level of the sluiceway of the dam was maintained such that the native species in the stream could readily move upstream, but perch would be excluded.

Angling within the study area was negligible: in 1953–55, 75, 151, and 73 trout were removed and following that, the average annual catch was 20 fish through 1965. Stocking consisted of only three minor experimental plantings and all fish released were marked. The section of stream below the study area is also private and little fished prior to 1958. After that date angling increased, reducing the trout population below the Wilcox Dam to an unknown degree.

A technique for efficient electrofishing was not developed until midway through the study. However, information on the standing crop of brook trout at this time served to fix the order of magnitude of the population. Excluding young-of-the-year (fish less than 10 cm), estimates for the years 1960–63 were 800, 435, 530, and 560 trout per kilometer with standing crops of 25, 15, 19, and 21 kg/ha. It was not feasible to obtain comparable estimates for non-trout species, but these did not appear excessively abundant. (Flick, W. A., and D. A. Webster. Fish Management Reports, Brandon Park, for the years 1960–1963 [multilith]).

Facilities and Procedures

Five stream traps were operated between mid-May and mid-November (Fig. 1). Upstream traps on the barrier dams of Wolf and Long Ponds were of the inverted-V type located underneath the inclined screen of the downstream trap or a short distance downstream. The upstream trap at these barrier dams caught mostly non-trout species. Fences were operated at Wolf Pond Camp Bridge and Pine Bridge with upstream or downstream trapping facilities at the sides. The lowermost trap at Wilcox Dam consisted of a modified inclined screen trap for capture of upstream or downstream migrants (Webster 1956). A low catch of minnows was observed in the downstream trap at this location, possibly because of the subsurface discharge. A fence at the top of the spillway sometimes overflowed, allowing undetected downstream movement. The several trapping facilities were in operation for varying periods as indicated in Table 1.

TABLE 1. Number (hundreds) and weight (kg) of trout, suckers, and minnows taken in Long Pond Outlet fish traps, 1953–65. Not operated a full season in 1953, 1956, 1959. Catch Index based on numerical catch divided by all traps operated for non-trout species and main stream traps only for trout since catch of trout at barrier dam traps negligible.

	Main stream traps			Barrier Dam traps		Suckers		Minnows		Brook trout		Catch Index	
Year	Wilcox	Pine Bridge	Camp Bridge	Long Pond	Wolf Pond	No.	Weight	No.	Weight	No.	Weight	Non-trout	Trout
1953	×			×	×	8.7	205.0	3.7	39.5	4.8	—	4	5
1954	×			×	×	3.9	152.9	10.1	55.8	8.5	34.0	5	8
1955	×			×	×	4.6	230.4	14.6	60.3	8.3	33.6	6	8
1956	×		×	×	×	7.4	139.2	25.2	60.3	9.9	40.6	8	10
1957	×		×	×	×	4.1	130.6	22.3	119.8	23.0	97.5	7	12
1958	×		×	×	×	1.1	47.2	10.9	92.1	24.5	85.4	3	12
1959	×		×	×	×	4.9	131.1	26.5	154.7	16.8	64.4	8	8
1960	×		×	×	×	1.0	36.7	6.0	44.0	9.2	44.4	2	5
1961	×		×	×	×	1.0	34.0	6.0	85.3	6.1	30.3	2	3
1962	×	×	×			.9	29.9	2.6	25.8	6.2	28.7	1	2
1963	×	×	×			.3	9.1	.9	13.2	5.3	21.0	<1	2
1964	×	×	×			.3	19.0	.9	20.9	6.7	25.6	<1	2
1965	×	×	×			.7	32.6	.6	8.2	1.4	5.1	<1	1
Total						39.1	1198	130.4	780	130.2	511		

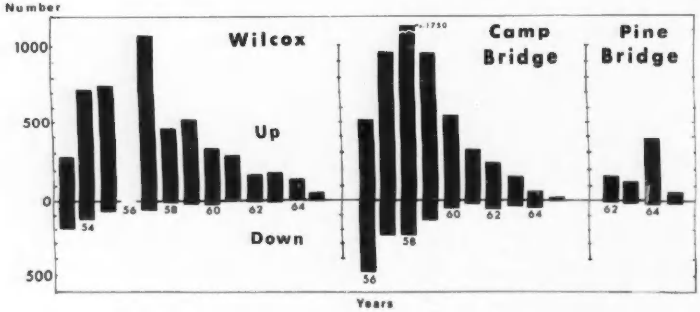


FIG. 2. Annual upstream and downstream catch of brook trout (*Salvelinus fontinalis*), Wilcox, Camp Bridge, and Pine Bridge traps, Long Pond Outlet, 1953–65. Traps not operated a full season in 1953, 1956, and 1959.

Trout were also captured by angling (fly fishing), wire traps (¼-inch mesh, 76 × 30 cm in diameter), and electrofishing. The high resistivity of the water (20,000–40,000 ohms/cm^3) necessitated the use of cattle salt blocks to improve conductivity; even so, a 500-V DC, 2.3-kw generator was required to fish effectively. Efficiency of electrofishing averaged 51% under favorable conditions, based on the recovery of 989 marked fish 10–25 cm in length (ranged from 44 to 59% for size categories within this range and not correlated with length).

Trout over 15 cm were tagged with a #3 mandible ring (in some instances smaller fish were finclipped), and, if caught in stream traps, passed in the direction of movement. Individual lengths (to the nearest 0.1 inch), weights (to the nearest 0.01 lb), and scale samples were taken from the lateral line area below the insertion of the adipose fin. Annuli were well defined on most scales and age determination seemed to offer no special problems. A Walford line based on tagged fish at large for 1 yr did not differ significantly from one based on mean lengths at age n and $n+1$, providing confidence in the validity of growth data based on scales. Other fish were enumerated by species and weight, and destroyed. Traps were tended 3–7 times a week during periods of maximum fish movement, once a week at other times.

REMOVAL OF NON-TROUT SPECIES

Operation of the three mainstream traps and two upstream traps at barrier dams on headwater ponds caught about 170,000 suckers and minnows weighing 2000 kg during 1953–65 (Table 1). In the period 1953–59, the weight removed usually fluctuated between 17 and 25 kg/ha per year (15–22 lb/acre) for the 16.9 km of stream between Wilcox Dam and Long Pond, but dropped rapidly in later years. These rates of removal are of limited value in a yield sense, because the relationship of the catch in fixed traps to total population is unknown and because fish moving into the area represent biomass produced elsewhere.

The dramatic decrease in catch may be interpreted as due to a reduction in movement of these species, as indicative of a decline in abundance, or to both factors. Most of the fish were caught in advance of, or during spring spawning activities, thus providing a powerful control mechanism over reproduction. The location of the mainstream traps at three of the five rapids providing spawning habitat for minnows and suckers doubtless enhanced this effect. It seems improbable that the phenomenon was secular in nature. Similar declining catch patterns in the Wilcox and Camp Bridge traps, separated in space by 8.8 km of stream, and in time of initiation of operation by 4 yr, suggest that the changes were the result of the removal program. The Pine Bridge trap did not begin operation until late in the study and the total catch in 4 yr was 2257 minnows and 87 suckers. Since it was located only about 2.4 km below the Camp Bridge trap, a negligible catch seems consistent with the overall low catch in the other traps at that time.

The lack of precontrol sampling by electrofishing precludes arriving at a firm conclusion in favor of an absolute decline of non-trout species. However, only 6, 8, 2, and 6 suckers, respectively, were electrofished in the 2.1-km section between Pine Bridge and Camp Bridge traps in 1960–63, indicating that suckers were a minor component of the population in that section during that period. Minnows were not effectively sampled by electrofishing in this stream, so there are no comparable observations on abundance.

Movement

The brook trout catch in the two mainstream traps at Wilcox Dam and Camp Bridge showed a marked decline during the 13 yr of observation (Table 1 and Fig. 2). When rough adjustments are made for the number of traps in operation, as suggested by the Catch Index in Table 1, the number of trout handled annually was reasonably stable in the period 1953–59, but thereafter diminished to a much lower level.

Movement was strongly directional upstream at all three mainstream traps. It was concentrated in spring and autumn, with the spring catch heavier in 9 of 12 yr when complete observations were available. Spring catches generally made up 50–70% of the total, the summer catch accounting for less than 10%. Some downstream movement took place during winter or early spring when traps were not operated as evidenced by recycling fish. Smith and Saunders (1958) noted some brook trout moved in early winter when water temperatures were near freezing.

Marked fish provided specific evidence on the pattern of upstream movement. The following schedule shows the proportion of trout tagged at Wilcox that were logged past the Camp Bridge trap during the same season:

Yr	1957	1958	1959	1960	1961	1962	1963	1964	1965
No. tagged	539	353	239	222	233	90	122	71	22
% recaptured	30	33	11	40	20	6	1	2	0

As the two traps were separated by 6.6 stream km, upstream orientation was well defined. The schedule also reflects the decline in movement in later years already noted in the gross trap catches, and suggests less extensive movement as well. Recaptures at the upper trap were mostly from tags placed in the spring and 92% of the total recoveries were made within 1 mo; over 40% were recovered within a week.

The contrast between fish moving up vs. downstream, was shown in data collected at the Camp Bridge site in 1958, when all fish were distinctively marked (trout under 15 cm were given a distinctive fin clip). Only 1% of 1750 trout moving upstream were recovered moving back down during the same season. Contrasting with this, 79% of 233 fish moving down were recaptured returning upstream. This suggested relatively localized movement for these fish, indicative of a resident as well as migratory segment of the population. This was confirmed in 1958 and 1961 when trout were tagged at intermediate points between Wilcox and Camp Bridge traps. The proportions subsequently recovered at Camp Bridge are clearly different:

	Tagged at Wilcox Dam	Tagged between Wilcox Dam and Camp Bridge
No. tagged	472	243
No. recovered at Camp Bridge	160	17
% recovered	34	7

Five times as many Wilcox-tagged fish were recovered at the upstream Camp Bridge trap, leading to the conclusion that migrating fish were not representative of the total population. The data for fish tagged at intermediate stations are biased on the high side because some of these fish were unrecognizable as moving fish. The existence of two groups, movers and nonmovers, was thus identifiable during the early years of observation, but about 1960, the strong annual spring pattern of upstream migration decreased coincidentally with a similar phenomenon in non-trout species. The virtual cessation of the extensive movements of all species of fish may have been due to an increase in living space resulting from the removal of non-trout species noted in the early years. Smith and Saunders (1967) found a marked change in the movement of brook trout in Ellerslie Brook following the construction of a pond near the estuary. A pond apparently substituted for the habitat previously offered by the estuary.

Most other studies suggest limited movement of stream populations of brook trout. Newell (1958) noted predominantly upstream movement in the torrential Oliverian Brook, New Hampshire, but the fish trap did not function in periods of high spring runoff and other freshets. Rupp (1955), McFadden et al. (1967), and Shetter (1936) conducted studies in which up- and downstream movement of at least the larger fish was about the same, and Shetter showed that trout moving downstream were usually recovered back upstream close to the tagging site.

Growth

Ages and growth characteristics of Long Pond Outlet trout were determined from scale samples of some 5500 specimens taken by various sampling methods. The length distributions of several large samples of trout taken in 1953–64 are broadly similar with the range in size lying between 8 and 25 cm (Fig. 3). Lack of homogeneity was often evident within the distributions and reflected differences in methods of capture, areas, and other vagaries of sampling. For example, conspicuous modes at 10–13 cm (representing yearling trout) are evident in the Camp Bridge samples in 1958, 1961–62, and 1964. Even so, length frequency distributions alone showed that substantive changes in length did not take place over the time span of the observations.

Age specific means generally showed reasonable consistency when samples taken by various methods were compared as typified by the following estimates of mean lengths (in centimeters with number of fish in parentheses) of age II fish in 1957–58:

Yr	Wilcox trap	Camp Bridge trap	Angling
1957	15.5 ± 1.8(89)	16.6 ± 1.3(33)	15.2 ± 1.8(93)
1958	15.7 ± 1.6(68)	15.0 ± 1.4(32)	15.0 ± 1.6(59)

Data were thus pooled by season of collection, and grand averages over the 13 yr computed

TABLE 2. Age-group means (centimeters) of brook trout taken by traps, angling, and electrofishing summarized by season of capture, Long Pond Outlet, 1953–65.

	Season					
	Spring		Summer		Autumn	
Age	No.	Length	No.	Length	No.	Length
I	244	11.3	373	12.8	768	13.3
II	1026	15.4	808	16.7	1128	17.3
III	546	19.6	264	20.6	262	21.7
IV	35	23.7	20	25.9	20	26.4
V	4	29.4	7	28.5	2	30.9

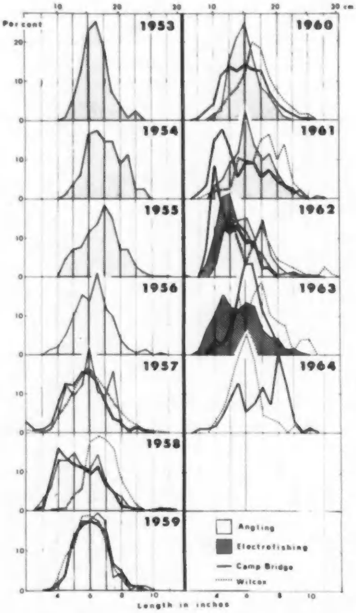


FIG. 3. Size distribution of brook trout taken by various sampling methods, July–September 1953–54, May–June 1955–64, Long Pond Outlet. Each curve based on >100 specimens.

(Table 2). The age-class means showed uniform annual increments of 4 cm/year from age I on. The discrepancy in between-age increments of 4 cm and within-season increments calculated from spring and fall means, about 1.9 cm, is because the midpoint of the spring sample was about June 1, well after the onset of the growing season. In 1957, when a larger early season sample of scales was available, 55% of 141 fish taken from April 28 to May 4 exhibited new 1957 growth; between May 4 and 24, 97% of 143 specimens showed new growth.

Age specific means and length–weight relationships were examined as a time series for evidence of improvement in growth or condition.

Spring and autumn mean lengths of age-groups I–III taken by all sampling methods were plotted using the grand class mean for 1953–64 as a reference (Fig. 4). No long-term trend was evident, the overall picture being one of fluctuations about the period average. A similar conclusion was reached from the comparison of length–weight relationships of trout at 2.5-cm intervals corresponding to 6, 7, and 8-inch size grouping. Analysis of covariance was used to compute an adjusted mean length for trout at 15.2, 17.8, and 20.3 cm for each of the sample years and these values were also plotted as a time series (Fig. 5).

Some parallel tendencies were evident in these parameters, especially in the arrays of calculated weights. Yearly means show highly significant differences from the overall averages, indicating that factors affecting growth were not static. The apparent initial upward trend in mean size of autumn samples of age II and III fish and the mean weights during the same period may be real, but because of data and design limitations, were interpreted as fortuitous in relation to a possible effect of removal of non-trout species.

These characteristics of slow growth and diminutive size have been evident in other upland stream studies, although influenced to a greater or lesser extent by removing older and larger fish by angling (Hoover 1939; Newell 1958; Seamans 1959; Lennon 1967; Warner 1970). One presumes a priori that paucity of food was the reason for slow growth, although comparative supporting data are not available for the populations studied. The species involved is also relevant, since brown trout (*Salmo trutta*) living sympatrically with brook trout exhibit better growth (for example,

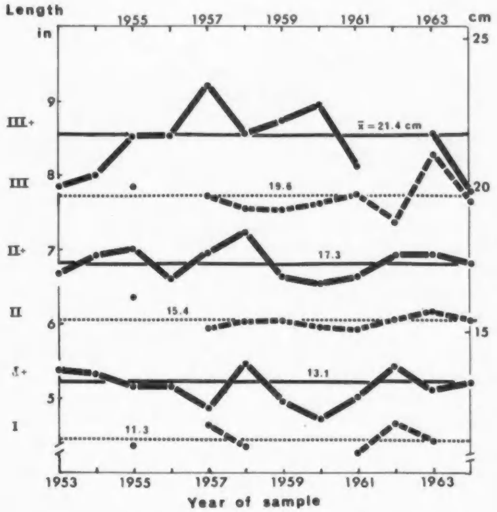


FIG. 4. Deviations of annual mean age-group lengths about the grand class mean for spring (*broken lines*) and autumn (*solid lines*) samples, 1953–64, Long Pond Outlet.

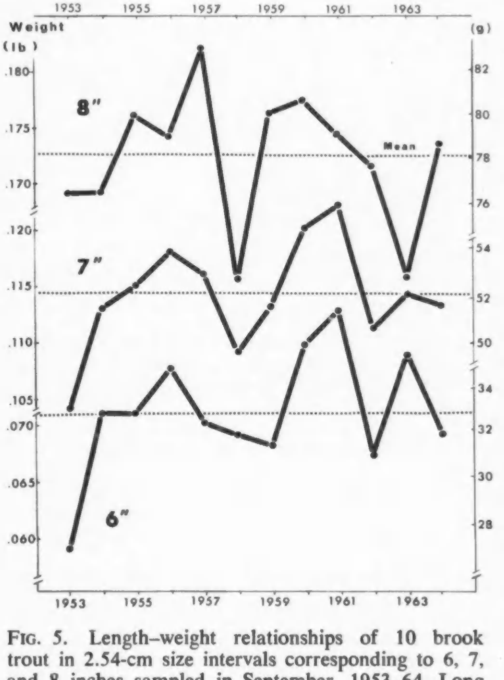


FIG. 5. Length–weight relationships of 10 brook trout in 2.54-cm size intervals corresponding to 6, 7, and 8 inches sampled in September, 1953–64, Long Pond Outlet.

Cooper 1953, as well as numerous New York State examples familiar to us).

Survival

Casual inspection of the age frequencies in the samples of brook trout from Long Pond Outlet was sufficient to indicate a high natural mortality rate from age II on (Table 2), since deaths due to angling were negligible. While a large number of age frequencies are available for examination, some problems arise in selection of an appropriate representative set of data for survival computations. The ratio of age III:age II fish in Table 2, for example, yields survival values of about 50, 33, and 24% for spring, summer, and autumn samples, respectively. Further breakdown by method of collection indicated that this sequence existed in fish caught by trapping and angling, but not electrofishing (19, 22, and 22% for the three seasons); hence, age frequencies in electrofishing samples were used to compute a weighted survival curve:

Age	I	II	III	IV	V
Frequency	774	1044	225	11	1

Age II was assumed to be completely vulnerable to sampling, although the frequencies of the older age-groups indicate different survival values, hence, are not informative on this point. The weighted annual survival between ages II and V was 18%. A high natural mortality rate was also suggested by the paucity of tag recoveries after 1 yr at large — only 170 of nearly 8900 tags placed; no second year recoveries were made.

Because of the variation imposed by method of capture and/or season of sampling, the data were judged not suitable for a meaningful examination of survival by year of collection. However, great changes would not be expected on the basis of the consistently steep-sided slope of the descending leg of the population length frequency distributions (Fig. 3).

It is not difficult to understand why the brook trout population in Long Pond Outlet was dominated by small fish since, in addition to slow growth, most died of natural causes after their third season of life, at lengths of 15.2–17.7 cm. This tendency has been noted in the studies cited on growth, although vulnerability of larger trout to even modest fishing pressure readily distorts older age frequencies.

Hatchery-reared offspring of Long Pond Outlet parents transplanted to nearby ponds showed much more favorable growth and survival, clearly demonstrating that neither the diminutive size nor an excessively high natural mortality rate were bound tightly to genetic influence (Flick and Webster Fish Management Reports, Brandon Park, for years 1960–1963 [multilith]). Similar observations on improved growth of transferred stunted trout were described by Greene (1955).

Migration out of the area by older and larger fish would have artificially inflated the mortality rate, but the size and age composition of trout caught in traps indicated this did not occur in Long Pond Outlet. Unusual predation or disease by pathogens or parasites does not seem a likely explanation in this or other situations studied. The possibility most worthy of further study is that poor nutritional state of the fish contributed to excessively high mortality. Evidence presented by Reimers (1963) and Hunt (1969) suggests that overwinter survival is, in part, at least, related to fat reserves.

Longevity and slow growth are not incompatible, as indicated by the unusual records of brook trout of 15 yr in alpine Bunny Lake (Reimers 1958, and personal communication quoted by Calhoun 1966), and 7–10 yr in Castle Lake (Wales and German 1956; Wales 1958). However, in these situations exceptionally slow growth and impaired sexual maturity in mitigated lake environments probably had a significant relation to longevity.

Conclusions

Removal of potential competitors for food and space did not influence growth of stunted trout in Long Pond Outlet, or the effect was not detectable in the data available. Perhaps compensatory factors were involved or abundance of non-trout species was not limiting under the environmental or size conditions involved. The cessation of the strong spring upstream movement of all species suggested at least a behavioral response to the removal of non-trout species. McFadden et al. (1967) showed that the population of brook trout in Hunt Creek was remarkably stable in growth and density over a comparable time span, and reduction of a population of stunted brook trout in a small Pennsylvania stream produced little change in the growth of the trout repopulating the area (Cooper et al. 1962). The environments in the streams referred to vary widely and, except for small size, seem to have little in common that can be related to characteristics of their trout populations. Although the factors limiting growth are obscure, removal of non-trout species does not seem a viable management technique for improving growth or survival of brook trout in infertile small streams.

Acknowledgments

We thank Mr and Mrs D. P. Ross, owners of Brandon Park, for support and opportunity to carry out the work on Long Pond Outlet. Field data in 1953–56 were collected by Mr H. Cook. Mr R. H. Kimpton Jr., superintendent of Brandon Park, assisted in the construction of stream traps, barrier dams, and in many other ways. Dr W. D. Youngs, Assistant Professor, Department of Natural Resources, Cornell University, assisted with some of the computations. Dr M. W. Smith, formerly of the Fisheries Research Board of Canada, St. Andrews, N.B., reviewed and commented on an early draft of the manuscript. Our colleague, Dr J. Forney, Director of the Cornell University Biological Laboratory at Oneida Lake, has been helpful in providing critical suggestions for the final draft. Finally, Mrs B. W. Little has been responsible for most of the clerical and graphical effort.

Cooper, E. L. 1953. Growth of brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in the Pigeon River, Otsego County, Michigan. Pap. Mich. Acad. Sci. Arts Lett. 38: 151–162.

Cooper, E. L., J. A. Boccardy, and J. K. Andersen. 1962. Growth rate of brook trout at different population densities in a small infertile stream. Progr. Fish. Cult. 24: 74–80.

Greene, A. F. C. 1955. Will stunted brook trout grow? Progr. Fish. Cult. 17: 91.

Hoover, E. E. 1939. Age and growth of brook trout in northern breeder streams. J. Wildlife Manage. 3(2): 81–91.

Hunt, R. L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. J. Fish. Res. Board Can. 26: 1473–1483.

Lennon, R. E. 1967. Brook trout of Great Smoky Mountains National Park. Bur. Sport Fish. Wildl. (U.S.) Tech. Pap. 15. 18 p.

McFadden, J. T., G. R. Alexander, and D. S. Shetter. 1967. Numerical changes and population regulation in brook trout *Salvelinus fontinalis*. J. Fish. Res. Board Can. 24: 1425–1459.

Newell, A. E. 1958. Trout stream management investigations of the Swift River watershed in Albany, New Hampshire. N.H. Fish Game Dep. Surv. Rep. 7: 40 p.

Reimers, N. 1958. Conditions of existence, growth, and longevity of brook trout in a small, high-altitude lake of the eastern Sierra Nevada. Calif. Fish Game 44: 319–333.

1963. Body condition, water temperature, and over-winter survival of hatchery-reared trout in Convict Creek, California. Trans. Am. Fish. Soc. 92: 39–46.

Rupp, R. S. 1955. Studies of the eastern brook trout population and fishery in Sunkhaze Stream, Maine. J. Wildlife Manage. 19: 336–345.

Seamans, R. G. Jr. 1959. Trout stream management investigations of Saco River watershed. N.H. Fish Game Dep. Surv. Rep. 9: 71 p.

Shetter, D. S. 1936. Migration, growth rate, and population density of brook trout in the North Branch of the

Au Sable River, Michigan. Trans. Am. Fish. Soc. 66: 203–210.

SMITH, M. W., AND J. W. SAUNDERS. 1959. Movements of brook trout, *Salvelinus fontinalis* (Mitchill), between and within fresh and salt water. J. Fish. Res. Board Can. 15: 1403–1449.

1967. Movements of brook trout in relation to an artificial pond on a small stream. J. Fish Res. Board Can. 24: 1743–1761.

WALES, J. H. 1958. Castle Lake investigation — progress report for 1957. Calif. Dep. Fish Game, Inland Fish. Admin. Rep. 58-6: 27 p. (Mimeo)

WALES, J. H., AND E. R. GERMAN. 1956. Castle Lake investigation – second phase: eastern brook trout. Calif. Fish Game 42: 93–108.

WARNER, K. 1970. Age and growth of brook trout, *Salvelinus fontinalis*, in some northern Maine streams. Copeia 1970: 358–360.

WEBSTER, D. A. 1956. Modifications of the Wolf-type fish trap. N.Y. Fish Game J. 3: 199–204.

A Revised Interpretation of the History of the Skeena River Sockeye Salmon (*Oncorhynchus nerka*)

W. E. Ricker and H. D. Smith

*Department of the Environment, Fisheries and Marine Service, Pacific Biological Station,
Nanaimo, B.C. V9R 5K6*

Ricker, W. E., and H. D. Smith. 1975. A revised interpretation of the history of the Skeena River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 32: 1369–1381.

Three factors are examined as an aid to interpreting the historical sequence of Skeena sockeye catches. One of these (Exploitation Mechanism 1) affects the catch directly, the other two affect catch by way of increasing or decreasing the recruitment produced by a given number of spawners. "Exploitation Mechanism 1" of Ricker (1973) makes the catch taken from any given brood during a time of increasing rate of exploitation greater than when exploitation is steady or decreasing; this is the main reason for excellent catches from 1905 to 1925. "Exploitation Mechanism 2" makes the progeny of any given number of spawners less numerous under conditions of maximum sustainable yield than during the period when rate of utilization is increasing; as a result recruitments observed prior to 1930 overestimate the potential productivity of the system and hence the sustainable yield. Mechanisms 1 and 2 are both operative even if the best rate of exploitation is never exceeded. In fact, however, the rate of exploitation began to exceed the optimum level of 50–55% about 1908, continued to increase until 1928, and then slowly decreased until the optimum level was reached about 1945; during the latter period, and for about 15 yr subsequently, catches were further depressed as spawning stocks were slowly rebuilt. Another factor affecting recruitment is the apparent existence of interaction between neighboring year-classes in respect to survival rate. Although the exact mechanism of this interaction is not yet known, it has produced three sequences of moderately "dominant" year-classes, the most recent being 1959–63–67–71, in spite of the complication of having two important ages of maturity for Skeena sockeye. More important is the fact that during the recent period large spawnings (0.75–1 million) have produced poor returns while moderately small spawnings (0.25–0.5 million) have produced larger year-classes than they did at any earlier period — in spite of the handicap of Mechanism 2. This apparent interaction between broods implies that one or more small spawnings are a necessary prerequisite for unusually successful reproduction by a later large one, and that successful large spawnings depress the reproduction of subsequent smaller ones. When all these factors are considered together, the observed trend of the Skeena catches can be reproduced. Maximum natural sustainable yield from the system would have been achieved about 1960 except for 2 yr of much reduced reproduction caused by the Babine River rock slide of 1951. Currently, the increased numbers of fry produced in artificial spawning channels at Babine Lake have contributed to large smolt runs that are now beginning to appear in the adult catches.

Ricker, W. E., and H. D. Smith. 1975. A revised interpretation of the history of the Skeena River sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 32: 1369–1381.

Nous examinons trois facteurs aidant à interpréter la séquence historique des prises de saumon nerka de la Skeena. Un de ces facteurs (Mécanisme d'exploitation 1) affecte les prises directement, les deux autres les affectent indirectement en augmentant ou diminuant le recrutement produit par un nombre de géniteurs donné. Le « Mécanisme d'exploitation 1 » de Ricker (1973) fait que la prise prélevée à même une portée donnée durant une période d'augmentation du taux d'exploitation est plus grande que lorsque l'exploitation est uniforme ou en voie de diminution; c'est la raison principale des excellentes prises de 1905 à 1925. Le « Mécanisme d'exploitation 2 » fait que la progéniture d'un nombre de géniteurs donné est moins nombreuse dans des conditions de rendement maximum soutenu que durant une période d'augmentation du taux d'utilisation; comme résultat, les recrutements observés avant 1930 surestiment la productivité potentielle du réseau et partant le rendement soutenu. Les Mécanismes 1 et 2 sont tous deux opératifs, même si le meilleur taux d'exploitation n'est jamais dépassé. En fait, cependant, le taux d'exploitation commença à dépasser le niveau optimum de 50–55% vers 1908, continua à augmenter jusqu'en 1928, pour ensuite diminuer lentement jusqu'à ce que le niveau optimum fusse atteint vers 1945; durant cette dernière période et environ les 15 années qui suivirent, les prises continuèrent à diminuer, en même temps que se rétablissaient lentement les

Printed in Canada (J3575)
Imprimé au Canada (J3575)

stocks reproducteurs. Un autre facteur affectant le recrutement est la présence apparente d'une interaction entre des classes d'âge voisines sous le rapport du taux de survie. Bien que nous ne connaissions pas encore le mécanisme exact de cette interaction, elle produisit trois séquences de classes d'âge modérément « dominantes », les plus récentes étant celles de 1959–63–67–71, et ceci en dépit de la complication créée par l'existence de deux âges importants de maturité chez le saumon de la Skeena. Fait plus important, durant la période récente, des fraies abondantes (0.75–1 million) donnèrent de maigres résultats, alors que des fraies modérément faibles (0.25–0.5 million) produisirent des classes d'âge plus abondantes que durant une période antérieure — en dépit du handicap du Mécanisme 2. Cette apparente interaction entre les portées laisse supposer qu'une ou plusieurs fraies peu abondantes sont une condition essentielle d'une reproduction réussie inusitée, et que d'abondantes fraies réussies abaissent le taux de reproduction des fraies suivantes moins abondantes. Bien que tous ces facteurs soient considérés ensemble, il est possible de reproduire la tendance observée dans les prises de la Skeena. Le rendement maximum soutenu naturel du réseau aurait été atteint vers 1960, sauf pour 2 années de faible reproduction causée par l'éboulis de la rivière Babine en 1951. Présentement, les nombres accrus d'alevins produits dans les chenaux de fraie artificiels ont contribué à une forte production de smolts qui commencent à apparaître dans les prises d'adultes.

Received September 24, 1974
Accepted April 18, 1975

Reçu le 24 septembre 1974
Accepté le 18 avril 1975

THE commercial fishery for Skeena sockeye (*Oncorhynchus nerka*) began in 1877. Average landings reached a peak about 1910 and remained at a high level during the next decade (Milne 1955, Table 4; Anon. 1962, Append. 2, fig. 2). During the 1920s, however, catches began to decrease in spite of a continued increase in fishing effort (Anon. 1962, Append. 2, fig. 3). Effort began to decrease in 1929, and the catch stopped declining 10 yr later. During the next 15 yr stocks gradually increased (Fig. 1), but the effects of a rock slide in 1951–52 sharply reduced the recruitments and catches of 1955–57 and to some extent in the generation following. Intensive management since that time has not been able to bring the catches at all close to the levels that prevailed between 1905 and 1925. Recent landings (1968–71) were in fact only about 45% as large as those of the system's best 4-yr period, 1908–11.

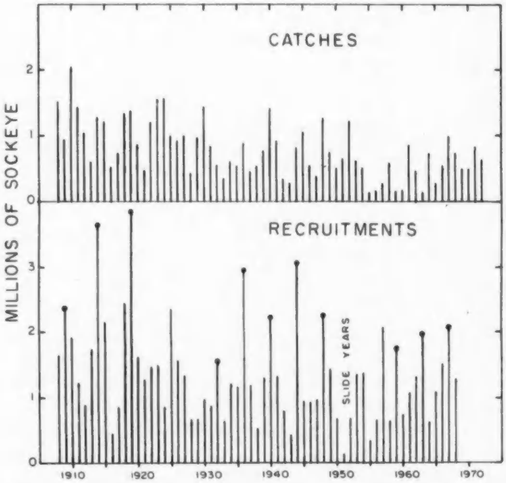


FIG. 1. Commercial catches and estimated total recruitments of Skeena sockeye salmon (*Oncorhynchus nerka*) of the one-lake-year life-history type. Catches exclude fish taken in Areas 3X and 3Y. Recruitments also exclude these, but include spawning stocks and subsistence catches. Recruitments are centered over the year of spawning, so are 4–5 yr out of phase with the catches. Solid dots represent regular sequences of "dominant" populations.

This failure to regain the level of yield characteristic of earlier years has been a great disappointment to all concerned. It is true that the Skeena's performance is no worse than that of most other large rivers; in fact, it is better than average. On the Fraser River, for example, the 1968–71 catch was about 34% of the record 4-yr yield established in 1899–1902. In Alaska the yields of most of the large sockeye systems have declined more than those of British Columbia. It is of course cold comfort to learn that neighbors are having troubles similar to your own, but this can and should stimulate enquiry as to whether there may not be common factors in operation.

Of the various reasons that have been suggested for present reduced levels of sockeye landings, this paper considers the following three for which some direct or indirect evidence exists concerning the Skeena:

1. *Exploitation Mechanism 1.* Catches from a given spawning escapement or from a given rate of exploitation are automatically and unavoidably greater during a phase of increasing exploitation than during a phase of steady or declining exploitation (Ricker 1973).
2. *Exploitation Mechanism 2.* Where stocks of different productivities are fished in common, the recruitment obtained from any total num-

ber of spawners is greater when rate of exploitation is increasing than when it is steady or decreasing (Ricker 1973).

3. *Interaction between year-classes*. There appear to be interactions between year-classes such that, if a sequence of unusually large generations (a "dominant line") exists, the productivity of the smaller lines is reduced, or vice versa.

Skeena Stocks and Recruitments

STOCKS

Aro and Shepard (1967) list 18 "major" stocks of sockeye in the Skeena system, a major stock being defined as one that had 5000 or more spawners at least once during 1951–62. There are also 20 or more "minor" stocks. Twelve of the major stocks, including the largest ones, are in the Babine River watershed. To some extent the various stocks have different migration times (Larkin and McDonald 1968; Smith and Jordan 1973), and in recent years early-running stocks at Babine Lake may have been increased slightly by reduced fishing during that part of the run. However, at any given time throughout most of the run the fish from a fairly large number of stocks will be taken together in the fishermen's nets.

Both in the major and the minor categories the various Skeena stocks differ greatly in abundance. A majority probably were never very large, and today some of the minor ones average only a few hundred spawners. But it should not be assumed that the present relative abundance of these stocks reflects the primitive situation at all closely. Rather we should expect the least productive stocks to have decreased greatly, while the most productive ones might even have increased their recruitments, though not their spawning contingents. A reflection of these events may possibly be found in the increase in percentage of 2-freshwater-year fish in the commercial catches during 1930–45, followed by their decrease to below the original level (Ricker 1968, fig. 7). Also, since 1944 there has been a 70% decrease in absolute abundance of non-Babine stocks in the escapement, for which there is no obvious cause other than differential reaction to fishing pressure.

RECRUITMENT CURVES

A device for representing the performance and potential of a salmon stock is the reproduction curve or recruitment curve, a plot of average catch-plus-escapement against the spawning stock that produced it. Among other things, a recruitment curve indicates the productivity of a stock, defined as the ratio of maximum sustainable yield (C_s) to average abundance before commercial fishing began (P_r) (Ricker 1973). Productivity, in this sense, is not directly related to the absolute abundance of a stock; there can be productive small stocks and unproductive large ones, though the latter quickly decrease in size when a fishery is begun.

Several recruitment curves have been fitted to the data for Skeena sockeye. Shepard and Withler (1958) divided successive catches of the system into age categories using age determinations available back to 1912, and so assigned each age-group of recruits to its corresponding spawning; estimates of the subsistence catch by Indians were included. The escapement was also estimated and similarly divided, and was added to the catch so as to obtain an estimate of the total fish produced by each spawning. They dealt only with the fish having 1 yr of freshwater life; this is the principal type on the Skeena and almost the only type in the Babine watershed, where they amounted to 96.6–99.8% during 1961–70. An empirical curve was fitted to these data on the basis of running averages (Fig. 2). Later information was added to this graph by Shepard et al. (1964), while Ricker (1968) added a few more years and fitted

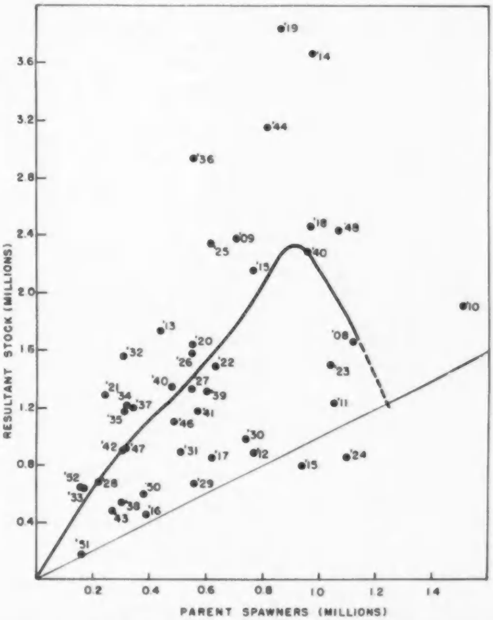


FIG. 2. Recruitment of Skeena one-lake-year sockeye of the brood years 1908–52, with a fitted empirical curve. (After Shepard and Withler 1958, fig. 2.)

TABLE 1. Escapements and returns of one-year-in-the-lake sockeye salmon (*Oncorhynchus nerka*) of the Skeena River for brood years 1940–67, in thousands of fish.

		Return at age 4_2					Return at age 5_2					Total return (omitting 3X + 3Y)	
Brood year	Effective escapement	Escapement	Area 4 catch	Subsistence catch	Total	3X + 3Y catch	Escapement	Area 4 catch	Subsistence catch	Total	3X + 3Y catch	R	R/E
1940	963	330	324	19	674		713	801	27	1541		2215	2.30
1941	572	227	254	9	490		369	451	24	844		1334	2.33
1942	305	117	90	4	211		239	319	31	589		800	2.62
1943	272	68	58	5	131		139	164	4	307		438	1.61
1944	824	927	1117	26	2070		359	607	35	1001		3071	3.73
1945	940	121	130	8	259		273	393	32	698		957	1.02
1946	486	120	106	9	235		252	429	18	699		934	1.92
1947	307	243	221	9	473		230	259	9	498		971	3.16
1948	1066	849	958	34	1841		137	264	15	416		2257	2.12
1949	480	570	343	20	933		206	292	20	518		1451	3.02
1950	393	304	206	11	521		62	93	10	165		686	1.75
1951	176	25	24	3	52		50	19	6	75		127	0.72
1952	237	320	125	37	482		127	76	15	218	9	700	2.95
1953	700	321	191	38	550	11	407	379	45	831	47	1381	1.97
1954	511	412	203	24	639	44	598	128	28	754	23	1393	2.73
1955	87	201	27	6	234	5	49	69	11	129	4	363	4.17
1956	370	224	92	14	330	23	172	158	8	338	17	668	1.81
1957	448	763	701	38	1502	67	241	305	19	565	75	2067	4.61
1958	819	318	154	10	482	27	114	36	12	162	2	644	0.79
1959	799	483	88	29	600	10	578	541	28	1147	38	1747	2.19
1960	273	270	172	9	451	13	131	143	19	293	10	744	2.73
1961	936	488	127	17	632	31	166	270	19	455	34	1087	1.16
1962	558	231	266	18	515	39	268	532	20	820	167	1335	2.39
1963	597	347	461	17	825	146	473	647	36	1156	121	1981	3.32
1964	848	92	87	5	184	23	208	229	16	453	35	627	0.75
1965	619	443	261	18	722	33	182	179	16	377	15	1099	1.78
1966	397	487	322	30	839	31	335	330	28	693	22	1532	3.86
1967	616	467	487	42	996	33	540	515	35	1090	65	2086	3.39

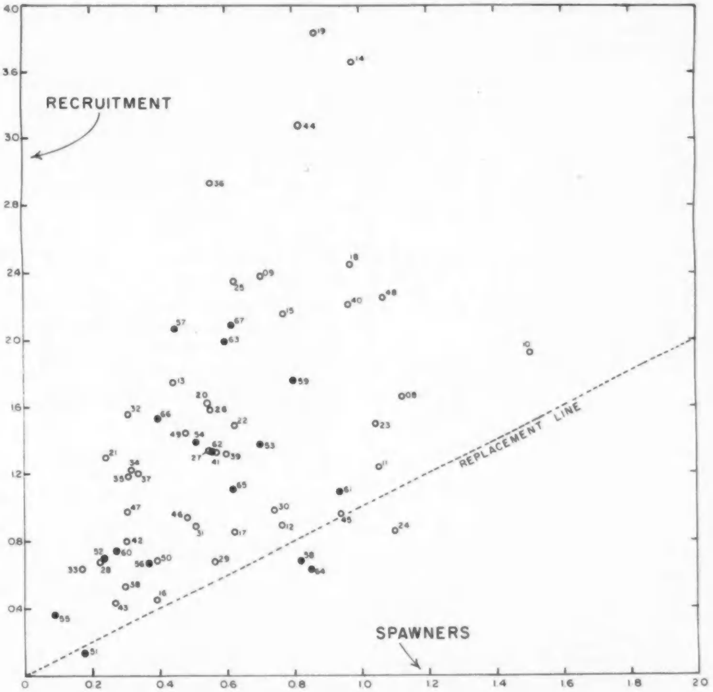


FIG. 3. Estimated spawnings and recruitments of one-lake-year Skeena sockeye (life-history types 4_2 and 5_2), in millions of fish. Commercial catches outside of Statistical Area 4 are excluded. Numbers show the year of spawning; spawnings since 1951 are in black. Data through 1939 are from Shepard and Withler (1958); more recent data are from Table 1.

several possible arbitrary curves. Allen (1973) used the same data to fit three mathematical curves.

The escapement and yield data for 1940–67 are given in Table 1. A small adjustment must be made to the figures for spawnings from 1965 onward, because an artificial spawning channel began to operate in that year. Based on rates of survival in the channels and in nature, the figures in the second-last column of Table 1 can be adjusted to give the probable return from natural propagation only. In thousands of fish, they are: 1965 — 1093, 1966 — 1349, 1967 — 1846.[1]

Figure 3 is a plot similar to Fig. 2, for spawnings from 1908 through 1967. In order to maintain comparability, the commercial catch included in Fig. 3 is limited to that of Statistical Area 4.[2]

Runs and Harvests

ARITHMETIC OF EXPLOITATION

The two exploitation mechanisms of Ricker (1973) apply to all salmon fisheries. Because of them, every fishery unavoidably fails to maintain its peak level of yield, quite apart from the direct

---

[1] There have been revisions of both escapements and catch estimates since 1940. Table 1 is not completely up to date for the years 1963–67, but the changes are very minor. Data for the brood year 1968 have become available since the paper was prepared. An escapement of 565,000 sockeye produced a recruitment of 1,298,000; R:P = 2.30.

[2] Since 1957 the catches in two Statistical Areas, 3X and 3Y, lying north of Area 4, have become available separately from the rest of Area 3. These include some Skeena River fish, as shown by their time of migration and their life-history type determined from the scales. Table 1 shows the catch of Skeena-type fish from these two areas; they increase the mean Skeena catch during 1958–72 by 13.9% and the mean total recruitment by 6.4%. Present commercial fishing boundaries in the Skeena region are shown in fig. 7 of Todd and Larkin (1971), while those of former years are in fig. 1 of Milne (1955).

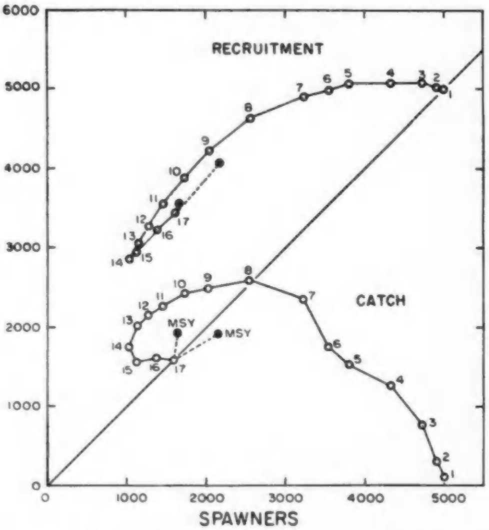


FIG. 4. Recruitment and catch in a model mixture of five stocks of unequal productivity, when subjected to the successive 5-yr average rates of exploitation that prevailed on the Skeena River. Successive "generations" are numbered. MSY indicates the two levels of almost-equal maximum sustainable yield that exist for this model. (From Ricker 1973, fig. 5.)

effect of any period of overexploitation, or of any deterioration of environmental conditions. Exploitation Mechanism 1 is simply the fact that the catch taken from the recruits produced by a given spawning is greater when rate of exploitation is increasing than when it has been decreasing (Ricker 1973, fig. 1). This applies either to single stocks or to mixtures of stocks. Exploitation Mechanism 2 is the fact that the recruitment produced by a mixture of stocks of unequal productivities (having different values of C_R/P_r) is greater when exploitation has been increasing than when it has been decreasing (Fig. 4). This is independent of and additional to Mechanism 1. Recruitments and catches during periods of unchanging rate of exploitation are of course intermediate (Ricker 1975, fig. 12.7).

Failure to recognize these two effects has made it difficult to understand the course of events on the Skeena. Mechanism 1 is apparently the more important one quantitatively, but it affects catches only, not recruitments. Mechanism 2 is not easy to grasp intuitively, and its magnitude depends on the number and relative productivities of the stocks that existed when commercial fishing began. The normal expectation is that the various salmon stocks of a river would exhibit a wide range of relative productivities. At one extreme, sockeye are able to occupy severe environments where, on the average, recruitment is barely sufficient to reproduce their parent spawners, so that little or no sustainable yield is possible. At the other extreme are environments so favorable that they potentially can support fisheries that take 70% or more of the recruitment at maximum sustainable yield, in which event that yield may equal or exceed the number of fish in the primitive stock. Approximate data for several groups of Skeena stocks during 1962–66 indicate that differences in the ratio of recruits to spawners do exist at present rates of exploitation (H. D. Smith and F. P. Jordan unpublished data), and these differences would necessarily have been greater when commercial fishing began. Thus it is wrong to expect a mixture of stocks to behave like a single stock which, when fishing pressure is relaxed, will rebound along the same recruitment curve that it travelled during the expansion phase. The mixture, by contrast, will trace a new and lower recruitment line in the course of its return to any lower rate of fishing (Fig. 4).

The net effect of these two mechanisms is that observed recruitments and catches have to be interpreted in the light of their position in the history of the fishery. For the same reason a trend line fitted to all the points in Fig. 3 would be of little value.

EXPLOITATION MECHANISM 1 AND OVEREXPLOITATION

Exploitation Mechanism 1 indicates that catches will be above sustainable levels when rate of exploitation is increasing, and below sustainable levels when it is decreasing. It is not necessary that the best rate of exploitation be exceeded, but if this occurs, Mechanism 1 continues to operate into the overexploitation range: it delays the decrease in catch that overexploitation implies, and it also delays the restoration of equilibrium catch when fishing is reduced. Ricker (1973) calculated a series of 5-yr mean rates of commercial exploitation for the Skeena from Milne's (1955) data, as follows: 1870–74, 0.02; 1875–79, 0.06; 1880–84, 0.15; 1885–89, 0.25; 1890–94, 0.30; 1895–99, 0.35; 1900–04, 0.48; 1905–09, 0.56; 1910–14, 0.59; 1915–19, 0.62; 1920–24, 0.64; 1925–29, 0.65; 1930–34, 0.67; 1935–39, 0.61; 1940–44, 0.53; 1945–49, 0.50; 1950–54, 0.46. Experience since 1945 is that a rate of exploitation between 0.5 and 0.55 is needed for maximum sustainable yield on the Skeena; this range was first significantly exceeded in 1910–14, it continued to increase through

1930–34, and only in 1940–44 did it return to the optimum level.

Exploitation Mechanism 2

One obvious aspect of Fig. 3 is that there were more large recruitments in earlier years than recently. To illustrate this more clearly the series has been divided into four periods:

Period	Spawnings	Remarks
Early	1908–28	Recruitments were subject to increasing rates of exploitation.
Middle	1929–50	Recruitments were subject to decreasing rates of exploitation or had not yet become equilibrated after the decrease ended in 1944.
Slide years	1951–52	Recruitments small because two thirds of the Babine fish were blocked, and many that got through were damaged by delay or overexertion.
Recent	1953–67	Rates of exploitation had no sustained trend up or down.

During the Recent period the stocks may still have been somewhat depressed by the earlier interval of overexploitation, because complete equilibration to the best rate of exploitation can be a protracted process (Ricker 1973).

Within the three major periods spawnings have been averaged in classes 250,000 broad; they and the corresponding mean recruitments are plotted in Fig. 5. Comparing the Early and Middle periods, we find that in almost every abundance-class of spawners the recruitment is greater during the Early one.[3] (The only exception is the largest class, for which there is only one spawning in the Middle period.) Such a difference is what is to be expected from Exploitation Mechanism 2, which causes recruitments from a given spawning (the R:P ratios) to be larger during a period of increasing exploitation than during a period of decreasing exploitation. The mean difference between the Early and Middle periods for the three central abundance classes is 11%; this is within the range of magnitudes obtained from models using several different mixtures of stocks, although it is somewhat larger than what can be measured from Fig. 4.

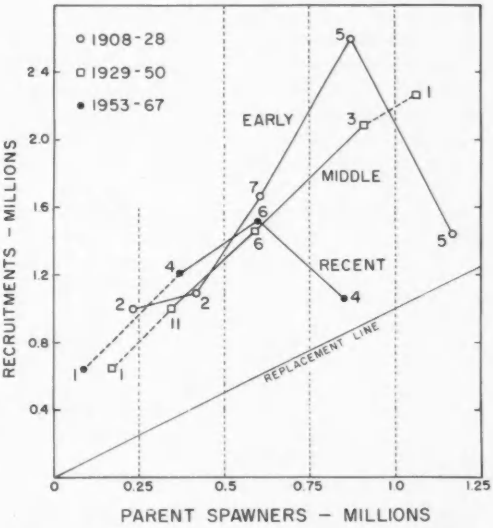


FIG. 5. Data of Fig. 3 divided into three periods and averaged within spawning classes 250,000 fish wide (1951 and 1952 are omitted). Numbers indicate the number of spawnings averaged in each group.

Combination of Mechanisms

If we compare the *catches* of the Early and Middle periods, both Mechanism 1 and Mechanism 2 come into play, so that in the Middle period a substantially smaller catch is to be expected from any given level of spawning — of the order of 20–35% smaller in Fig. 4, which of course is not the maximum possible effect.

As mentioned earlier, the optimum rate of exploitation was exceeded from about 1908 to 1941. For about 15 yr after 1908 the effect of overexploitation in reducing recruitment was masked by the continued increase in the percentage of the recruits that were caught, so that the catch was maintained. By the early 1920s however, this could no longer compensate for the reduced abundance of fish, and catches fell off. Toward the end of the decade, when fishing effort stopped increasing, the effects of Mechanisms 1 and 2 were superimposed on the reduced absolute abundance of spawners, and by the middle 1930s the mean catch had fallen to less than half of its peak level. From 1940 to 1955 recruitments increased gradually, while catches remained about the same because rate of exploitation was lower.

Thus the history of mean recruitments and mean catches up to 1955 can be explained adequately in terms of the mechanics of exploitation and the amount of fishing that took place.

---

[3] Ricker and Manzer (1974, fig. 16) divided the spawnings into two sequences, 1908–40 and 1941–61 (including 1951 and 1952), and the earlier of these was superior in all categories of spawnings. However, the division point selected was largely arbitrary. The three-period division used in Fig. 5 is related to changes in the trend of rate of exploitation, the "slide" years are omitted, and the Recent period includes 6 yr of observations not available to Ricker and Manzer.

What is not explained is the variability in recruitment from year to year. This might be ascribed entirely to environmental variability, but for the fact that persistent sequences of above-average recruitments can be observed in Fig. 1, which have some resemblance to the well-known sockeye cycles of the Fraser River.

Interaction Between Year-Classes

DOMINANT LINES

During three episodes of the history of the Skeena runs there have been sequences of years when one parent-progeny line maintained a consistent numerical superiority (Fig. 1). Five-year-old fish produced a strong series from the spawnings of 1909, 1914, and 1919, while 4-year-old fish mainly accounted for the strong year-classes produced by the spawnings of 1932, 1936, 1940, 1944, and 1948. In recent years a new 4-year sequence has started with the spawnings of 1959, 1963, and 1967, in spite of a management policy that aims at bringing all year-classes up to a high and more or less uniform level.[4] However, up to now fish in the dominant broods of the Recent period have been less numerous than those of both the previous episodes.

The shift from 5-yr to 4-yr dominance occurred during the 1920s, probably influenced by the fact that the 5-yr fish, being larger, were more heavily exploited than 4 yr olds and so were at a disadvantage in reproducing their kind under this type of fishing regime[5] (Larkin and McDonald 1968; Todd and Larkin 1971). The 4-yr sequence of the 1930s and 1940s was terminated in 1952 by the Babine River slide; this affected the 1951 and 1952 spawnings directly, and was followed by a period of irregular production up to 1959. The latter apparently represents a "jockeying for position" among the different lines, and was complicated by the fact that 5-yr-old fish had acquired some advantage from the rock slide in 1951 and 1952, because larger fish passed the slide more readily than smaller ones (Godfrey et al. 1954).

The first two of these dominant lines or "cycles" on the Skeena have long been evident, but it has been uncertain whether any active mechanism of interaction is involved. Larkin and McDonald (1968) discussed the problem and made computer simulations for the Skeena similar to those of Larkin (1971) for the Fraser. Although their assumptions did not reproduce some features of the observed sequence of catches, they did indicate the possibility of interaction between year-classes. The appearance of another dominant line in recent years gives new support to the idea that dominance is an integral feature of the system.

CAUSES OF DOMINANCE

The only known theory of dominant lines that is consistent with the available facts postulates that the largest survival rates from fry to adult occur when a year-class becomes abundant enough to escape the control of one or more agents, most likely predators or parasites, that keep other year-classes small (Ricker 1950; Ward and Larkin 1964). At the same time, the abundant year-class temporarily increases the numbers or effectiveness of the controlling agent, so that subsequent year-classes are attacked more heavily and thus produce recruits at a lower rate. These smaller year-classes in turn reduce the abundance of the control agent(s) through malnutrition or because of reduced opportunities for a parasite to find its host, thus setting the stage for another large year-class. This sequence implies that at a high level of abundance some different agent or effect controls the dominant lines themselves — possibly poor survival of eggs in overcrowded spawning grounds, or debility from insufficient food during lake life.

A corollary of the above position is that if there happens to be no dominant line in existence at a particular time, spawnings of smaller sizes should produce at a better rate than when an unusually large year-class is occurring every 4 or 5 yr. This is because the control agent has no chance to become unusually abundant in years of unusual abundance of fingerlings.

There is no direct evidence for interaction of this type on the Skeena, but the sequence of recruitments in Fig. 1 has two features that may be suggestive. First, during the three dominance episodes observed to date there have been sequences of two to four generations in which the smallest brood became smaller as the dominant line became progressively larger, and vice versa. However, the year 1940 is less than the two adjacent maxima, and both the 1921 and the 1947 minima fail to follow the trend. Thus the picture is not good evidence for interaction, but complete absence of any suggestion of a reciprocal relation between large years and small could be considered evidence against it.

---

[4] The Babine smolts from the next spawning of the dominant series, 1971, were 56% more numerous than any other brood since such observations began, although part of this excellent production can be ascribed to the increased fry output from artificial spawning channels. In any event it appears that this dominant line is likely to persist for at least one more generation.

[5] There is no implication here that age of maturity is completely determined by parental age, merely that a hereditary component exists and that the mean age of a stock can be modified by selection. For evidence on heritability of age of maturation of Skeena sockeye see Milne (1955) and Godfrey (1958); and for the genus *Oncorhynchus* as a whole see Ricker (1972).

The second suggestive aspect of Fig. 1 and 3 concerns the spawnings of the two slide years, 1951 and 1952. In both years the number of spawners was small, the sex ratio favored males, and the females were in poor condition — quite a number died unspawned or partly spawned (Godfrey et al. 1954). However, the 1951 spawning failed to reproduce itself ($R:P = 0.7$), whereas R:P was 3.0 for 1952. This is in agreement with the hypothesis of interaction. In 1952 the control agent(s) would be at a level of abundance corresponding to previous more or less normal sockeye populations, so that the 1951 brood experienced no relief from their pressure. However, the small number of young sockeye present in 1952 decreased the abundance of the control agent(s), so that in 1953 the 1952 brood was attacked much less severely and could show a much better R:P ratio (Fig. 3).

YEAR-CLASSES SINCE 1952

The poor recruitments from the 1951 and 1952 spawnings made it necessary to reduce fishing in 1955–57 in an effort to obtain an adequate number of spawners. Moderately good escapements were in fact obtained, although the year-class produced by the 1955 spawning was still weak. Following this, an attempt was made to obtain spawning escapements in the range 800,000–900,000 whenever there were sufficient fish, because that was the level indicated for maximum sustainable yield on the recruitment curve of Fig. 2. Four such spawnings were obtained, but the results were very disappointing; on the average they did little more than reproduce their own numbers (Fig. 5). By contrast, the smaller abundance-classes of spawners have produced more recruits recently than did similar spawnings during the Middle period and (on the average) even slightly more than during the Early period (Fig. 5). This latter is in spite of the effect of Mechanism 2, which (if other things had been equal) would have made the Recent recruitments substantially less than those of 1908–28 at all levels of spawner abundance.

Shepard and Withler (1958) had available to them essentially the data for the Early and the Middle periods. Their empirical recruitment curve (Fig. 2 here) increases its slope in the range of spawning stocks from 650,000 to 900,000; this puzzled them, because it is contrary to ordinary theoretical expectation, which is that R:P should decrease with increasing stock size. With all the years' data that are now available, a corresponding objective empirical curve would be much smoother, and the small hump that remains in the 900,000–1,000,000 spawner range could reasonably be ascribed to random fluctuation in success of reproduction. What has happened is that the very good recruitments from the 1914, 1918, 1919, and 1944 brood years are now balanced by the very poor recruitments from the 1945, 1958, 1961, and 1964 brood years (Fig. 3).

However, to us it seems highly unlikely that the difference between the Shepard–Withler recruitment line and the present overall average picture can be ascribed solely to random fluctuations in survival. Rather, the recruits produced by spawnings larger than 750,000 have decreased substantially, while during the same period the recruits produced by smaller spawnings have increased in spite of a mechanism that tends to reduce them. It is difficult to believe that these two phenomena are not somehow related.

Regulation of Abundance and Yield

COMBINATION OF INTERACTION AND THE EXPLOITATION MECHANISMS

During the first half of the Early period the dominant broods of the year-classes 1909–14–19 achieved very high levels of recruitment, as did one adjacent brood — 1918 (Fig. 3). Hence, on any theory of interaction we should expect that some or all of the smaller year-classes had their survival rates unfavorably affected during that time. However, the rate of exploitation was increasing, so the recruitments from a given spawning mostly remained fairly large because of Mechanism 2 (Fig. 3), while the catches were much larger, relatively, because of the additional effect of Mechanism 1. During the Middle period the rate of exploitation was decreasing, and the same two Mechanisms made the absolute levels of recruitment substantially lower (Fig. 5) and the catches much lower yet. However, the establishment and persistence of a new dominant line shows that the biological basis for interaction was as strong as ever.

The dominant year-classes of both periods were produced mainly by spawnings in the 750,000–1,000,000 range, whereas their presumed depressing effect operated on smaller spawnings. This interaction, plus the fact that

TABLE 2. Comparison of two indices of fingerling abundance (observed number of adult spawners and the smolts they produce) and mean smolt size with the mean incidence of *Eubothrium* in the smolt migration. The influence of the spawning channels begins gradually with the spawning of 1965 and increases through 1971. (See the text for sources of data.)

	Nilkitkwa L. and North Arm (Early smolt run)				Main Lake and Morrison L. (Late smolt run)				Combined		
Brood year	Adults (*thousands*)	Smolts (*millions*)	Weight (g)	Infestation (%)	Adults (*thousands*)	Smolts (*millions*)	Weight (g)	Infestation (%)	Smolts (*millions*)	Weight (g)	Infestation (%)
1949	352	—	—	—	60	3.88	5.60	—	—	—	—
1950	182	—	—	—	98	4.19	4.89	33	—	—	—
1951	25	—	—	—	67	2.78	6.19	38	—	—	—
1952	147	—	—	—	122	2.35	6.30	13	—	—	—
1953	277	—	—	—	228	23.62	5.35	6	—	—	—
1954	238	—	—	—	197	13.19	5.05	10	—	—	—
1955	19	—	—	—	29	5.20	5.91	—	—	—	—
1956[a]	119	14.40	4.88	19	159	8.40	6.06	25	22.80	5.62	21
1957	188	9.00	3.86	—	212	24.90	5.54	—	33.90	5.18	—
1958[a]	265	26.00	4.37	46	294	31.10	6.18	45	57.10	5.63	46
1959[a]	283	6.12	4.06	32	309	13.13	5.26	25	19.25	4.88	28
1960[a]	93	1.73	5.25	30	106	13.68	5.62	28	15.41	5.58	29
1961	370	6.75	4.38	—	346	7.71	5.33	—	14.46	4.81	—
1962[b]	254	16.54	4.43	—	142	29.35	5.32	—	45.89	5.00	—
1963	155	4.51	4.82	—	246	20.37	5.14	—	24.88	5.08	—
1964	270	21.53	4.20	25	338	13.77	4.68	37	35.30	4.39	31
1965	297	9.73	4.95	15	176	6.83	5.34	30	16.56	5.11	21
1966	184	12.79	4.57	20	108	18.10	4.53	26	30.89	4.55	24
1967	188	22.01	5.08	23	233	24.17	5.37	35	46.18	5.23	29
1968	236	8.40	4.91	6	242	34.60	5.08	14	43.00	5.05	12
1969	288	13.30	4.29	5	220	39.20	5.84	18	52.50	5.45	14
1970	266	8.78	4.91	11	298	44.89	5.31	31	53.67	5.24	28
1971	288	14.77	4.24	20	351	74.63	5.33	27	89.02	5.15	26

[a] *Eubothrium* infestation estimated from fingerling samples taken in the lake the previous year.

[b] The division between early and late smolt runs is doubtful.

large spawnings were much more numerous in the Early period when recruitments had not yet been reduced very much by Mechanism 2, evidently operated jointly to produce the ascending side of the steep hump of the recruitment curve of Fig. 2. The descending side reflects the rather poor recruitments obtained from four out of five spawnings larger than 1,000,000, perhaps caused by congestion of the spawning grounds.

POSSIBLE INTERMEDIARIES

In theory the mechanism of interaction between year-classes can be either direct or indirect. A direct mechanism is one where a large year-class reduces the survival rate of one or more subsequent year-classes, for example by exhausting their food supply or by direct cannibalism. An indirect mechanism is one where a small year-class results in reduced abundance of a control agent (predator or parasite) and this permits a subsequent year-class to have an excellent survival rate. At Babine Lake direct interaction on any significant scale seems practically impossible because a great majority of smolts leave the lake before the fry enter it. Also, in the sea, cannibalism is unlikely because sockeye feed mainly on plankton, and because during their early months at sea the small fish occupy a different region from the larger ones.

Concerning indirect interaction, considerable suspicion has been directed at the cestode parasite *Eubothrium salvelini* as an intermediary, because infected smolts have mean weights 18–35% less than those that are free of the parasite (Smith 1973, table 5). Thus heavy infestations might well cause mortality in the lake, directly or indirectly, and in addition smaller smolts have a lower survival rate than larger ones after they leave Babine Lake (H. D. Smith and J. McDonald unpublished data). However, it has not been possible to demonstrate any relation between incidence of infection and estimates of either the current year's or the previous year's sockeye population in the lake (Table 2).[6] Also, in the North Arm and Nilkitkwa Lake, where populations of fingerlings have been much denser and smolts are smaller (Table 2), infection of smolts has been somewhat less than in the main lake, particularly in recent years. It may be that *Eubothrium* could be a controlling agent without any positive correlation appearing. For example, when the initial infection was heavy most of the infected fingerlings might have died in the lake, so that unparasitized individuals would be the prinicpal survivors to the smolt stage. However, there is no evidence that this occurs, and at the present time it is impossible to know whether or not *Eubothrium* plays a role in the interaction cycle.

There are also other possible kinds of interaction. For Shuswap Lake sockeye the favored hypothesis is an interaction between sockeye and the predacious fish that consume them in the lake (Ward and Larkin 1964). On the Skeena a similar interaction might occur either within Babine Lake, or in the spawning creeks and rivers, or during estuarine or early marine life. It might also happen that infertile and dead eggs from a large spawning, which can persist in the redds for at least a year, would make succeeding spawnings less successful, as suggested by Hunter (1959) for pink and chum salmon. Unfortunately, there is at present no evidence for or against any of these possibilities.

ESTIMATE OF MEAN NATURAL RECRUITMENT AT MAXIMUM SUSTAINABLE YIELD

If the hypothesis of year-class interaction is correct, the recent absence of really large year-classes has been compensated at least partly by better returns from spawnings of medium size. Indeed the data suggest almost perfect compensation. The 22 spawnings of 1929–50 produced 1,310,000 fish each on the average, while the 15 spawnings starting in 1953 produced 1,280,000 — almost the same number. Both periods were handicapped: by the effects of previous and current (up to 1942) overexploitation in the Middle period, and by effects of the Babine River slide in the Recent period. Hence, under natural spawning conditions the system should have been able to reach an average equilibrium recruitment at a somewhat larger figure than either of these, perhaps 1,500,000, with a best rate of exploitation between 50% and 55%. But taking full advantage of hindsight, it now seems unlikely that average recruitment would ever have risen into the 2–2.25 million range.

FUTURE DEVELOPMENTS

Johnson (1961, 1965) showed that the main body of Babine Lake was producing zooplankton enough and contained space enough to support a population of sockeye fingerlings several times as large as was present during 1955–63. Starting in 1964, channels were constructed beside two of its spawning streams, and when operating at full capacity these can more than double the number of fry entering that part of the lake. In 1971 the channels operated at 72% of their final capacity, and they increased the number of smolts leaving the main lake to 75 million, whereas the largest prechannel figure was 31 million (Table 2). This 75 million was of course obtained in a dominant year of the Recent series, when good survival was to be expected on the basis of past performance.

---

[6] In Table 2, the division of adult escapements between the two lake regions is on the basis of annual counts and estimates by Fisheries Service personnel. The number of smolts and their mean weights are from data of J. McDonald and F. C. Withler for 1949–59, of H. D. Smith for 1960–70, and of the Fisheries Operations Branch for 1971. Data on incidence of *Eubothrium* infection are from table 1 of Smith (1973), with data for 1970 and 1971 added.

It is too soon to know what effect the additional fry from the channels will have on survival rates in other years. Johnson's (1961) graphs indicate that a 50% decrease in fingerling growth (to October) might be expected in the main lake when the population reaches 10 times the density of the 1956 year-class. This density was achieved by the 1971 year-class, if the ratio of smolt migrations can be taken as an indication; however, no decrease in smolt size was observed, nor was their *Eubothrium* infection unusual (Table 2).

Even if it is not *Eubothrium*, there must be some agency of interaction that explains the establishment and persistence of dominant lines, which under the new regime will assume control at, we hope, a much higher level than in the past. But eventually there may have to be a deliberate policy of maintaining different year-classes at greatly different levels of abundance in order to obtain maximum overall yield. Alternatively, nature herself may see to it that there are "off" years in the series.

Discussion

The two "Exploitation Mechanisms" considered in this paper are of general applicability, and will assist in interpreting the history of salmon catches from all large rivers. They do not, of course, constitute a complete interpretation. On the Skeena the phenomenon of interaction and the Babine rock slide must be taken into consideration, and on other systems similar or quite different phenomena may be important. Ricker (1968) listed 12 possible reasons for a sustained decrease in sockeye catches. These included what was later named Exploitation Mechanism 2, and also the interaction between year-classes, but did not include Mechanism 1. Some of the other points listed in 1968 are still possible contributors to the decline in overall productivity of Skeena sockeye. For example, there is the increase in the relative number of jacks and decrease in average size of the older fish, both due to selection of larger fish by the fishery; also, a decrease in basic productivity of some of the lakes of the system may have occurred because they are no longer so heavily fertilized by sockeye carcasses. However, none of these seem likely to be playing any important role as yet, because the exploitation mechanisms plus interaction can account for all of the changes not attributable to the two obvious causes — the Babine rock slide and the new spawning channels.

Considering the great practical significance of Exploitation Mechanism 2, it is surprising that it was first mentioned as recently as 1968 and not fully described until 1973. Actually several writers had been skating around the idea somewhat earlier. The fact that the salmon runs of large rivers are mixtures of many stocks has long been common knowledge. Ricker (1958) pointed out that if stocks of different productivities are fished together it is not possible to obtain as large a total catch as when each can be fished at its own best rate. Doi (1962) elaborated this by plotting the equilibrium yields from different mixtures of the spawning populations of two stocks that differ in productivity. Paulik et al. (1967) developed a complete analytical procedure for equilibrium yields, and illustrated it for a mixture of three stocks. The authors of all three of these papers were probably close to realizing that their work implied a progressive and permanent decrease in the ratio of recruitment to total spawners (R:P) during the developmental period of a fishery, but they all failed to make the point explicitly. Only a little reflection was needed to show that less productive stocks must decrease to a smaller fraction of their original abundance than more productive ones do, which is one way of describing Exploitation Mechanism 2.

Tanaka (1962) examined the relation of recruitment to spawning stock historically in several sockeye systems, using 5-yr running averages. For the Skeena he divided the escapements and returns into eight sequences, and arranged them into three groups according to two different systems shown in his fig. 5. For each of them Ricker-type reproduction curves were calculated, six in all. System I implies that density-independent mortality changes with time, and System II implies a change in density-dependent mortality. Actually neither type of mortality has changed appreciably, in any biological sense, but while the stocks of poorer productivity were being reduced the R:P ratios for the system were larger at all levels of stock, and their gradual decrease gives the appearance of an increase in density-independent mortality — Tanaka's System I. The central curve of Tanaka's fig. 5(I), around which his most recent observations cluster, indicates a very reasonable optimum rate of exploitation — 53%. However, the points in that figure shift from one line to another and, as Tanaka observes, "this seems to be unnatural." A "natural" interpretation for the original data is now provided by the two exploitation mechanisms, the effects of the Babine slide, and interaction between year-classes. Tanaka's paper is valuable in emphasizing the fact of historical change in the R:P ratio, but it contains no explanation of it.

Allen, K. R. 1973. The application of research to the management of British Columbia sockeye salmon. Trans. Am. Fish. Soc. 102: 172–177.

Anon. 1962. Report on salmon stocks of the Pacific coast of Canada with reference to Articles III(1)(a) and IV of the International Convention for the High Seas Fisheries of the North Pacific Ocean. Bull. Int. North Pac. Fish. Comm. Bull. 9: 1–67.

Aro, K. V., and M. P. Shepard. 1967. Salmon of the North Pacific Ocean — Part IV. Spawning populations of North Pacific salmon. 5. Pacific salmon in Canada. Int. North Pac. Fish. Comm. Bull. 23: 225–327.

Doi, T. 1962. On the reproduction curves and optimum escapements for the sockeye salmon stocks of the Skeena River, the Fraser River and Bristol Bay and the pink salmon stocks of Alaska. Bull. Int. North Pac. Fish. Comm. Bull. 9: 107–112.

Godfrey, H. 1958. A comparison of sockeye catches at Rivers Inlet and Skeena River, B.C., with particular reference to age at maturity. J. Fish. Res. Board Can. 15: 331–354.

Godfrey, H., W. R. Hourston, J. W. Stokes, and F. C. Withler. 1954. Effects of a rock slide on Babine River salmon. Bull. Fish. Res. Board Can. 101: 100 p.

Hunter, J. G. 1959. Survival and production of pink and chum salmon in a coastal stream. J. Fish. Res. Board Can. 16: 835–886.

Johnson, W. E. 1961. Aspects of the ecology of a pelagic zooplankton-eating fish. Verh. Int. Verein. Limnol. 14: 727–731.

1965. On mechanisms of self-regulation of population abundance in *Oncorhynchus nerka*. Mitt. Int. Verein. Limnol. 13: 66–87.

Larkin, P. A. 1971. Simulation studies of the Adams River sockeye salmon. J. Fish. Res. Board Can. 28: 1493–1502.

Larkin, P. A., and J. G. McDonald. 1968. Factors in the population biology of the sockeye salmon of the Skeena River. J. Anim. Ecol. 37: 229–258.

Milne, D. J. 1955. The Skeena River salmon fishery, with special reference to sockeye salmon. J. Fish. Res. Board Can. 12: 451–485.

Paulik, G. J., A. S. Hourston, and P. A. Larkin. 1967. Exploitation of multiple stocks by a common fishery. J. Fish. Res. Board Can. 24: 2527–2537.

Ricker, W. E. 1950. Cycle dominance among the Fraser sockeye. Ecology 31: 6–26.

1958. Maximum sustained yields from fluctuating environments and mixed stocks. J. Fish. Res. Board Can. 15: 991–1006.

1968. Background information and theory related to management of the Skeena sockeye salmon. Fish. Res. Board Can. MS Rep. 961: 38 p.

1972. Hereditary and environmental factors affecting certain salmonid populations, p. 27–160. *In* R. C. Simon and P. A. Larkin The stock concept in Pacific salmon. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C.

1973. Two mechanisms that make it impossible to maintain peak-period yields from stocks of Pacific salmon and other fishes. J. Fish. Res. Board Can. 30: 1275–1286.

1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 188: 382 p.

Ricker, W. E., and J. I. Manzer. 1974. Recent information on salmon stocks in British Columbia. Int. North Pac. Fish. Comm. Bull. 29: 1–24.

Shepard, M. P., and F. C. Withler. 1958. Spawning stock size and resultant production for Skeena sockeye. J. Fish. Res. Board Can. 15: 1007–1025.

Shepard, M. P., F. C. Withler, J. McDonald, and K. V. Aro. 1964. Further information on spawning stock size and resultant production for Skeena sockeye. J. Fish. Res. Board Can. 21: 1329–1331.

Smith, H. D. 1973. Observations on the cestode *Eubothrium salvelini* in juvenile sockeye salmon (*Oncorhynchus nerka*) at Babine Lake, British Columbia. J. Fish. Res. Board Can. 30: 947–964.

Smith, H. D., and F. P. Jordan. 1973. Timing of Babine Lake sockeye salmon stocks in the north coast commercial fishery as shown by several taggings at the Babine counting fence and rates of travel through the Skeena and Babine Rivers. Fish. Res. Board Can. Tech. Rep. 418: 1–31.

Tanaka, S. 1962. Studies of the question of reproduction of salmon stocks. Int. North Pac. Fish. Comm. Bull. 9: 85–90.

Todd, I. S., and P. A. Larkin. 1971. Gillnet selectivity on sockeye (*Oncorhnychus nerka*) and pink salmon (*O. gorbuscha*) of the Skeena River system, British Columbia. J. Fish. Res. Board Can. 28: 821–842.

Ward, F. J., and P. A. Larkin. 1964. Cyclic dominance in Adams River sockeye salmon. Int. Pac. Salmon Fish. Comm. Progr. Rep. 11: 116 p.

Changes in Abundance and Certain Biological Characteristics of Grand Bank American Plaice, *Hippoglossoides platessoides*

T. K. Pitt

Department of the Environment, Fisheries and Marine Service, Newfoundland Biological Station, St. John's, Nfld. A1C 5X1

Pitt, T. K. 1975. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides*. J. Fish. Res. Board Can. 32: 1383–1398.

Commercial exploitation of American plaice on the Grand Bank increased from the early 1950s reaching a peak of about 90,000 tons in the mid-1960s. Catches have subsequently declined to about 45,000–50,000 tons annually. The increased exploitation of plaice was reflected in declines in catch per hour and stock abundance of fully vulnerable age-groups and an increase in the rate of instantaneous fishing mortality (F). The documentation of these was particularly strong in ICNAF Division 3L, but appeared to be somewhat erratic in 3N, probably because of incomplete sampling of the stock prior to the mid-1960s.

Average size at age increased gradually from the early 1950s to the 1970s apparently because of increased growth rate in the initial 2 or 3 yr of life. Coupled with the increased size at age were significant declines in the age at sexual maturity.

Significant correlations were found between stock abundance and asymptotic length (L_∞), and size at age 5 and 10 in Division 3L and while positive trends could be demonstrated between some of these and mean bottom temperature, the correlations were not significant.

Pitt, T. K. 1975. Changes in abundance and certain biological characteristics of Grand Bank American plaice, *Hippoglossoides platessoides*. J. Fish. Res. Board Can. 32: 1383–1398.

L'exploitation commerciale de la plie canadienne sur le Grand banc est allée en s'accroissant depuis le début des années 1950 et atteignit un sommet d'environ 90,000 tonnes vers le milieu des années 1960. Les prises ont ensuite diminué à environ 45,000–50,000 tonnes annuellement. L'exploitation accrue de cette espèce a entraîné une diminution des prises par heure et de l'abondance des groupes d'âge pleinement vulnérables, et une augmentation du coefficient instantané de mortalité due à la pêche (F). Ceci a été démontré de façon particulièrement convaincante dans la division 3L de l'ICNAF, mais quelque peu irrégulière dans la division 3N, probablement à cause d'un échantillonnage incomplet du stock avant le milieu des années 1960.

La taille moyenne à un âge donné a augmenté graduellement depuis le début des années 1950 jusqu'aux années 1970, en apparence à cause d'un rythme de croissance plus rapide durant les 2 ou 3 premières années de vie. Associée à une plus grande taille à un âge donné, on a constaté une diminution significative de l'âge de la maturité sexuelle.

Nous avons trouvé des corrélations positives significatives entre l'abondance du stock et la longueur asymptotyque (L_∞), et la taille aux âges 5 et 10 dans la division 3L. Bien que nous ayons pu démontrer des tendances positives entre certains de ces paramètres et la température moyenne de du fond, les corrélations ne sont pas significatives.

Received December 11, 1974
Accepted April 21, 1975

Reçu le 11 décembre 1974
Accepté le 21 avril 1975

In the past decade American plaice (*Hippoglossoides platessoides*) has become one of the major commercially exploited groundfish species in the northwest Atlantic. For the Canadian fishery on the Grand Bank (International Commission for the Northwest Atlantic Fisheries [ICNAF] Divisions 3L, N, and O), especially the Newfoundland-based trawlers, it is of particular importance accounting for up to two thirds of the trawler landings of groundfish in some years.

The greatest abundance of American plaice in the northwest Atlantic occurs on the Grand Bank primarily at those locations of the bank that are strongly influenced by the Labrador current. The fishery directed primarily for plaice occurs in the shaded areas of Fig. 1 with the greatest yield coming from ICNAF Division 3L. Plaice are fished usually at 40–100 fath (73–183 m) in the northern part of the bank (Division 3L) and 40–150 fath (73–277 m) to the south (Division 3N) with some fishing also occurring in Division 30.

Heavy commercial exploitation, principally in

Printed in Canada (J3676)
Imprimé au Canada (J3676)

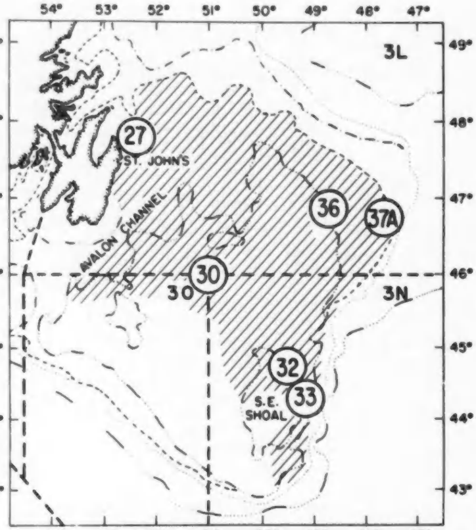


FIG. 1. Map showing ICNAF Divisions and places mentioned in the text.

Divisions 3L and 3N, has resulted in a reduction in stock size particularly of the mature, fully exploited fish. This reduction has apparently brought about certain biological changes and this paper attempts to document and analyze the change in density and relate it in particular to differences in growth that have occurred during an approximate 18-yr period.

Since the major fishery for this species by the Canadian fleet occurs primarily in Divisions 3L and 3N, this paper is based on data collected from these localities. It should be noted, however, that for management purposes the whole of the Grand Bank is considered as a single stock and as such is under international regulation through ICNAF (Pitt 1973a).

Materials and Methods

NOMINAL CATCHES

The compilation of total nominal catch was complicated because certain European countries up to 1972 reported their total landings of plaice, yellowtail flounder (*Lamanda ferruginea*), and witch (*Glyptocephalus cynoglossus*) as "unspecified flatfish." However, the ICNAF Secretariat in 1974 received a breakdown of the catches of the various flatfish by European countries for 1963–72 (Anon. 1974). For the pre-1963 period the separation of species was based on the proportions of these in Canadian landings.

An important omission in these data is the amounts of plaice discarded by certain countries that were fishing only for cod; thus, it is possible that Spanish pair trawlers catch quantities of flatfish that never appear in official statistics.

ESTIMATES OF FISHING EFFORT AND CATCH PER UNIT EFFORT

Information was obtained from fishing logs recorded on board most trawlers operating from Newfoundland ports. The Newfoundland-based trawlers catch a major proportion of the total plaice landings from the Grand Bank so that these log records are probably representative of the whole plaice fishery for this area.

The basic unit of fishing effort was the number of hours fished by Canadian stern otter trawlers 500–900 tons (ICNAF tonnage Class 5). Up to 1964–65 the Canadian fleet was composed almost entirely of side trawlers 151–500 tons (ICNAF tonnage Class 4). Since then, however, stern trawlers were phased in fairly rapidly so that by 1972 most of the fleet consisted of this type.

To convert earlier side trawler information to standard stern trawler equivalents, monthly catch per hour by Newfoundland side trawlers (Class 4) for individual unit areas were plotted against comparable data for stern trawlers (Class 5). The slope of the line of best fit drawn by eye, passing through the origin had a slope of 0.8 and the latter was used to convert Class 4 effort to Class 5.

Catch per hour was compiled in two ways (a) "main species plaice" from catch and effort data where plaice was taken in the largest quantities in relation to other species making up the catch from a particular trip from a single statistical area (directed fishery) and (b) "plaice recorded in catch" which uses all catches and effort where any quantity of plaice was caught.

Standardization of the USSR and other European landings by large factory trawlers (ICNAF Tonnage Class 6 and 7) presented difficulties since insufficient data were available to make comparison with Canadian catches. Total effort for ICNAF Divisions 3N and 3L was therefore estimated by dividing total reported catch of all countries by catch per hour by Canadian class 5 trawlers, i.e.

$$\text{Total effort} = \frac{\text{Total catch (All countries)}}{\text{Catch/h} \quad \text{Cdn.} \quad \text{Class 5 otter trawlers}}$$

SEPARATION OF STOCKS

Plaice from ICNAF Divisions 3L and 3N were treated as separate stocks. Tagging indicated that on the Grand Bank, plaice are relatively sedentary (Pitt 1969) with minimal migration between northern and southern sections of the bank. Thus very few plaice tagged on the northern slope near 46° N (Division 3L) were recovered south of 45° 30′ N (Division 3N). Similarly, of plaice tagged on the eastern slope 45° N very few were recovered north of 46° N latitude (Division 3L). Vertebrae counts (Pitt 1961) failed to give any basis for stock separation except to indicate that Flemish Cap plaice (ICNAF 3M) were probably discrete from those of the Grand Bank. Growth patterns for Divisions 3L and 3N were quite different with plaice from Division 3L being much smaller at comparable ages than those from Division 3N at any particular period (Pitt 1967).

SEPARATION OF THE SEXES

To estimate population size and growth changes separation of the sexes was necessary. Males are smaller than females at comparable ages from about age 7 or 8. Females have a longer life span and become sexually mature 5–7 yr later than males and at a larger size (Pitt 1966). Males are vulnerable to the gear and fully recruited to the fishery at a younger age than the females.

CALCULATION OF NUMBERS CAUGHT

Estimates of numbers caught at each age were based on samples from the Newfoundland commercial fleet. Up to the late 1960s, random length measurements were taken from commercial landings during 2-wk periods, normally on a quarterly basis, and fish selected for otolith sampling. More recently, stratified samples were taken from each 2-cm group based on a method described by Gulland (1955). Since both random and stratified samples were adjusted to the measured frequency, both methods gave comparable results; however, the stratified method gives better representation at the upper and lower length-groups.

The mechanics of estimating numbers caught first required raising the numbers measured at each 2-cm length-group to the total catch of the sampled boat by the ratio of the weights of the sampled boat and the sampled fish and then to the total numbers caught (quarterly or semiannually) at each length by the ratio of weight landed (total) and the weight of all sampled boats. In all cases the catch and landings were broken down by sex from the proportional weight of sampled fish. Finally, age-length keys were applied to the length frequency of total numbers to give the number caught at age.

When sufficient data were available, age-length keys were compiled for January–June and July–December to take care of possible growth during the year that could bias the results when adjusting to measured frequencies.

CALCULATION OF FISHING MORTALITY (F) AND STOCK SIZE

The method used was based on Baranov's (1918) catch equation

$$C_n = \frac{F}{Z_n}(1 - e^{-Z}n)\, N_n$$

where C = number of fish in the catch in year *n*, N_n = the number present at the beginning of the year, and F_n and Z_n, respectively, fishing and total mortality during year *n*.

The recent use of this method in fisheries assessment for which W. E. Ricker (personal communication) has suggested the title "Sequential Computation of the Rate of Fishing and Stock Size" developed from the "virtual population" method described by Fry (1949 and 1957) and modified by Gulland (1965). For the latter method only year-classes that have passed completely through the fishery can be used. Jones (1968) showed that by certain rearrangements of the basic equation, F could be calculated from the catch (C) of consecutive age-groups of individual year-class of a stock. The technique is essentially similar to that used by Ricker (1948) with incompletely vulnerable ages of halibut and was used in this assessment.

The Jones method, which is described in detail by Schumacher (1970) in an assessment of West Greenland cod (ICNAF Subarea 1), requires the following: (i) the total annual numbers caught (C) in each age-group, (ii) an estimation of the exploitation rate F/Z $(1-e^{-z})$, for the oldest age-groups, and (iii) an estimate of natural mortality (M).

Basically the Jones method involves a rearrangement of the Baranov equation, where Z = total, F = fishing and M = natural mortality, and C_n = catch in year *n* and N = number of fish in the stock at the beginning of the year.

$$\text{If } \frac{F}{Z} = (F/F + M) = E$$

then $C_n = E_n\,(1 - e^{-zn})\,N_n$ (Baranov catch equation)

and $C_{n+1} = E_{n+1}\,(1 - e^{-Z}n + 1)\,N_{n+1}$

but $N_{n+1} = N_n e^{-z}n$

using these relationships the ratio (C_{n+1}/C_n) can be rearranged to give

$$\frac{C_{n+1}}{C_nE_{n+1}\,(1 - e^{-Z}n + 1)} = \frac{e^{-Z}n}{E_n\,(1 - e^{-Z}n)}$$

Thus, with a given value for M and an estimated starting exploitation rate $(E_{n+1}\,(1-e^{-Z}n+1))$ for the oldest age-group, values of F can be sequentially calculated from the oldest to the youngest age-groups of a year-class, and stock size at the beginning of the year can then be calculated.

Although stock size was calculated separately for the sexes, they were combined in presenting total available numbers. The idea was to present only fully recruited fish. In Division 3L, full recruitment occurred at age 12 for males and 15 for females, whereas in 3N the corresponding ages were 10 and 13 yr. So as to include substantial quantities of males in the totals in addition to the age 15 fish and older, 13 and 14 yr olds were also included for Division 3L, and 11 and 12 yr olds in addition to the 13 yr and older in Division 3N.

Obviously the accuracy of stock size is dependent on estimates of numbers caught and as pointed out previously, because of the lack of data on discards, catch estimates are probably minimal and thus probably also the estimates of stock size. The discard of small plaice made the calculation of stock size in the lower age-groups especially difficult.

NATURAL MORTALITY (M)

Instantaneous natural mortality rates of 0.25 for males and 0.20 for females were used in estimations of fishing mortality and stock size. Several methods were used to calculate M (Pitt 1973a) such as total mortality of virgin stocks from St. Mary's Bay, Newfoundland, and Hamilton Inlet Bank; catch and effort data from ICNAF Divisions 3L and 3N using Beverton and Holt's (1957) iterative method and Paloheimo's (1961) linear formulae. The latter method utilizes total mortality (Z) from annual catch curves plotted on annual effort. Additionally, total mortality of a series of year-classes plotted against the effective effort (Paloheimo 1961) was also used. A summary of estimates of M from Pitt (1973) is as follows:

	Div. 3L		Div. 3N	
Method	♂	♀	♂	♀
Beverton and Holt (1957)	0.27	0.23	0.22	0.16
Paloheimo's (1961) linear formulae	0.22	0.23	0.17	0.18
Z from year-classes (Paloheimo 1961)	0.25	0.23	0.39	0.21
Avg	0.25	0.23	0.26	0.18

Total Z from catch curves of unexploited stocks

St. Mary's Bay — ♂ = 0.27
— ♀ = 0.18
Hamilton Inlet Bank — ♂ = 0.30
— ♀ = 0.22

COMPARISONS OF GROWTH CURVES

Because they have a longer life span than males and for simplicity in presentation, only female plaice were used in comparing growth curves for a series of years. Samples collected during the first half of the year only were used. Insufficient commercial data were available for 1969–72 to present curves for that period for Division 3N. Von Bertalanffy growth equations using a weighted least square fit (Allen 1966) were used. Research data were fitted from age 4 and over and commercial data from age 6.

The research data were secured by the vessel *A. T. Cameron* using a 41–5 otter trawl with a lined cod end. Total catches were used when these were small or random or stratified sampling of larger hauls. Except for 1971 and 1972 when fishing stations were selected by the stratified random method (Grosslein and Pinhorn 1971), fishing positions were at predetermined depths on transcepts across the slope of the bank.

AGE AND LENGTH AT SEXUAL MATURITY (M_{50})

The age at which plaice were sexually mature (M_{50}) was calculated using the procedure described by Bliss (1935a, b, 1952) in assessing the effects of various dosages of poisons and vitamins on animals. Fleming (1960) described the method as applied to the determination of age at 50% maturity for cod of the Newfoundland area and a similar procedure was used in an earlier paper (Pitt 1966) for plaice in the northwest Atlantic. In this paper calculations of M_{50} were made for a number of localities for the 1957–64 period including the northeast and southeast slopes of the Grand Bank corresponding roughly to ICNAF Divisions 3L and 3N, respectively. Determination of sexual maturity was similar to that described in the previous paper (Pitt 1966).

AVERAGE LENGTH RELATED TO STOCK ABUNDANCE AND BOTTOM TEMPERATURES

To relate the differences in size at age to the apparent change in abundance, the average length of female at selected ages and the asymptotic length grouping data in 4-yr periods were plotted on stock size averaged for the same combination of years for research data L_∞ and average length at ages 5 and 10. For commercial data, asymptotic (L_∞) length and length at age 10 were used. The same length data were plotted on mean bottom temperatures averaged for the appropriate stations in the respective ICNAF Divisions.

Changes in Abundance

TRENDS IN NOMINAL CATCH, 1955–72

In Division 3L annual landings increased very gradually from 1955 to 1966, reaching a level just below 20,000 tons. In 1967, landings increased sharply, reaching a peak of approximately 52,000 tons in 1969 then declined to about 20,000 tons in 1973 (Fig. 2). In Division 3N, catches in early years were around 5,000 tons, increased sharply in 1964, peaked at about 35,000 tons in 1966, then declined to around 15,000 tons in 1969. Since then, catches have averaged about 15,000 tons annually. On the southwest part of the Grand Bank (Division 30) except for large reported catches by the European fleet in 1966–69, as mentioned earlier, catches have remained generally below 10,000 tons.

The increase in plaice landings during the early and mid-1960s can be easily explained. Up to 1961–62, the haddock fishery was very important to Canadian and foreign fishing fleets. As haddock stocks declined and fishing by Newfoundland-based component of the Canadian fleet expanded, effort was directed to plaice, first in Division 3N and later in Division 3L. The European fleet, mainly USSR, fished primarily in Divisions 3N and 30 with much of the catch of plaice being a by-catch, probably in the fishery directed to catching cod. There is no indication that the increase in landings was because of improved availability of plaice.

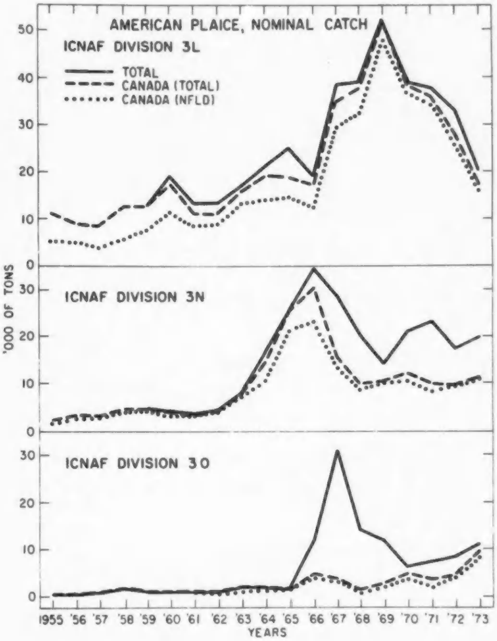


FIG. 2. Nominal catches of plaice from ICNAF Divisions 3L, 3N, and 30.

FISHING MORTALITY (F) FOR FULLY RECRUITED PLAICE

Estimates of F at corresponding ages were generally higher for males than females (Table 1). Although males were usually smaller at comparable ages, they apparently became vulnerable to capture earlier, since length frequencies for both research and commercial catches indicated a preponderance of males at the lower size-groups (Pitt 1973). The reason for this is not apparent, but the 50% maturity point for males is age 6 (about 24 cm) in Division 3L and age 5 (about 26 cm) in Division 3N, whereas for females it is 14 yr (40 cm) and 9 yr (41 cm) in Divisions 3L and 3N, respectively. Just how the early maturation of the males could result in earlier vulnerability is not clear. Males are fully recruited at age 11 in Division 3L and age 9 in Division 3N, whereas for females the corresponding ages are 15 and 13 yr (Pitt 1966).

Values of F in Division 3L were generally 0.15–0.25 for both males and females up to the early 1960s. For males the rate increased after 1961 to 1.18 in 1969 and 1.06 in 1970; however, these are probably aberrant since they were calculated from data producing values for ages 12 and 13 only. For females average values of F were generally lower, and peaked in 1960–70 at 0.55 (Table 1).

In Division 3N there was no real increase in F for males until 1966 when a value of 0.48 was calculated and the highest value 0.69 calculated for 1969 (Table 1). For females, F increased gradually from 0.10 in 1956 to 0.30 in 1965 with an overall upward trend giving a peak value of 0.50 in 1971.

CATCH PER UNIT EFFORT

A downward trend in catch per hour for both weight (Fig. 3A and Table 1) and numbers caught (Fig. 3B) was evident in Division 3L. Weight landed per hour declined from 1200 kg (plaice in catch) in 1955 to approximately 430 kg in 1971 and 1972 with a similar trend when plaice was the main species sought. For numbers caught per hour the trend is similar but slightly more irregular. The increase in numbers per hour for 1971 and 1972 can be attributed, in part at least, to the fact that more small fish were landed by the Canadian fleet than in previous years.

In Division 3N the trend up to 1964 is not clear, but from 1956 to 1962 there was an overall decline in the catch per hour (weight) (Fig. 3A and Table 1). The catch per hour increased from 700 kg in 1962 to 1050 kg in 1964 (plaice main species) followed by a general downward trend. For numbers caught per hour the pattern is similar except that the 1960 peak is more pronounced

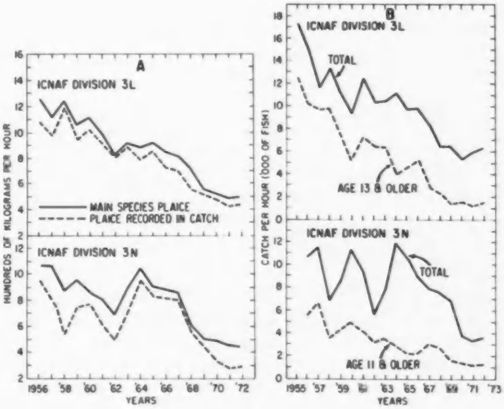


FIG. 3. A, Catch per hour (kilograms) by Newfoundland-based trawlers for Divisions 3L and 3N; B, catch per hour (numbers) for total catch and for fish 13 yr and older and 11 yr and older in Divisions 3L and 3N, respectively.

TABLE 1. List of catches, total effort, catch per unit effort, and average instantaneous fishing mortality (F) for plaice from ICNAF Divisions 3L and 3N. Values of F are for fully recruited fish for the ages shown.

	Division 3L							Division 3N						
				Male		Female					Male		Female	
Year	Nominal catch (tons)	Effort 1000s h	Catch/h (kg)	F	Ages	F	Ages	Nominal catch (tons)	Effort 1000s h	Catch/h (kg)	F	Ages	F	Ages
1955	11,518	7.3	1578	0.15	12–16	0.14	15–20	2,193	2.3	950				
1956	9,125	8.4	1083	0.16	12–16	0.19	15–20	3,162	3.3	952	0.12	10–14	0.10	13–18
1957	8,466	8.7	977	0.11	12–16	0.25	15–20	3,198	3.9	815	0.18	10–14	0.14	13–18
1958	12,745	10.7	1190	0.21	12–16	0.25	15–20	4,550	8.6	530	0.27	10–14	0.15	13–18
1959	12,656	13.5	940	0.29	12–16	0.27	15–20	4,506	6.0	749	0.30	10–14	0.17	13–18
1960	19,379	18.8	1030	0.25	12–16	0.23	15–20	3,912	5.1	774	0.30	10–14	0.15	13–18
1961	13,398	14.6	918	0.25	12–16	0.26	15–20	3,448	5.5	624	0.19	10–14	0.18	13–18
1962	13,584	16.9	802	0.31	12–16	0.30	15–20	3,923	7.9	499	0.19	10–14	0.18	13–18
1963	16,516	18.7	901	0.45	12–16	0.27	15–20	7,465	10.4	719	0.29	10–14	0.24	13–18
1964	20,909	26.4	792	0.47	12–15	0.26	15–20	14,587	15.1	964	0.25	10–14	0.24	13–18
1965	25,034	29.2	864	0.42	12–15	0.32	15–20	26,270	31.0	846	0.31	10–14	0.30	13–18
1966	18,572	25.2	737	0.47	12–14	0.31	15–20	34,698	41.8	829	0.48	10–14	0.37	13–18
1967	38,515	54.3	710	0.53	12–14	0.42	15–20	24,364	30.1	810	0.54	10–14	0.45	13–18
1968	39,726	68.8	568	0.83	12–14	0.47	15–19	20,038	35.2	570	0.69	10–13	0.45	13–17
1969	52,880	100.1	527	1.18	12–13	0.50	15–19	14,442	31.5	459	0.48	10–11	0.35	13–18
1970	39,347	87.4	449	1.06	12–13	0.55	15–20	21,032	61.9	340	0.56	10–11	0.44	13–18
1971	37,851	88.0	430	0.67	12–14	0.42	15–20	22,873	81.2	282	0.48	10–12	0.50	13–18
1972	33,330	74.1	447					17,387	58.0	300				
1973	20,103	41.6	483					20,883	64.6	323				

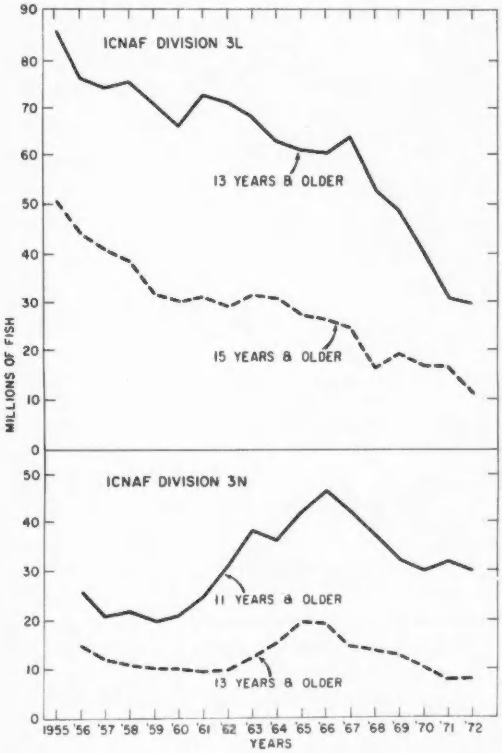


FIG. 4. Stock abundance 12+ and 15+ yr-old fish in Division 3L and 10+ and 12+ fish in Division 3N.

(Fig. 3B). As a further index of abundance the numbers caught of the older age-groups were also presented (Fig. 3B). For both Divisions a general downward trend is evident.

STOCK SIZE

An overall decline in stock abundance of fully recruited plaice (15 years and older) and at a slightly younger age (13 yr and older or 75–80% recruited) was evident in Division 3L (Fig. 4) for the period 1955–72. In Division 3N, however, the fully recruited stock appeared to decline from 1956 to 1962 then increase to reach a peak in 1965 and 1966, followed by a downward trend to 1972. With slightly younger fish included (11 yr and older, 75–80% recruited), the stock appeared to increase in abundance from 1959 and reached a peak in 1966, followed by a decline to the end of the period.

RELATING CATCH PER UNIT EFFORT TO ABUNDANCE

Since estimates of numbers present in the stock are most reliable for age-groups that are completely or nearly completely vulnerable to the gear, only these estimates were used here.

For Division 3L straight line relations can be demonstrated with highly significant correlation coefficients ($P<0.001$) for weight caught per unit effort, and numbers caught per unit effort (Fig. 5A and B) for the fully recruited (15 yr and older) and for the stock (13 yr and older). In Division 3N (Fig. 5A and B), although a significant correlation was found between stock size of fully recruited ages (13 and older) and weight caught per unit effort ($P=0.04$), no significant correlation could be demonstrated for the plot of fully recruited stock size on numbers caught per hour ($P=0.06$). For the younger age-group (11 and older) correlation coefficients were not significant for either relation ($P=0.5$ and 0.8, respectively). However, using just the data for 1962–72 did give significant correlation for both the weight caught per hour ($P=0.02$) and for numbers per hour ($P=0.04$).

These correlations seem to support the validity of the effort data used in calculating the catch per unit effort.

Growth Changes

COMPARISON OF GROWTH CURVES FROM RESEARCH AND COMMERCIAL DATA

A gradual overall increase in the elevation of growth curves indicating an increase in mean size at age was evident (Fig. 6 and Table 2). Curves for research and commercial data from the same ICNAF Division were slightly different since at younger ages, either through gear selectivity or discard, commercial vessels take a greater proportion of faster growing fish at the younger ages. At the upper end of the age scale the commercial fleet sometimes discards large old fish because of possible jellied condition of the fish muscle.

In Division 3L, in commercial data for 1969–72, the size at age to about age 12 was lower than in the two previous periods, possibly because recently, processors have accepted smaller fish with the resulting lowering of the discard rate.

DIFFERENCE IN SIZE AT AGE FOR SELECTED YEAR-CLASSES AND AGE-GROUPS

A comparison in mean size at age for 1954–55 and 1960–61 year-classes (Fig. 7) utilizing ages on the relatively straight line portion (ages 6–11

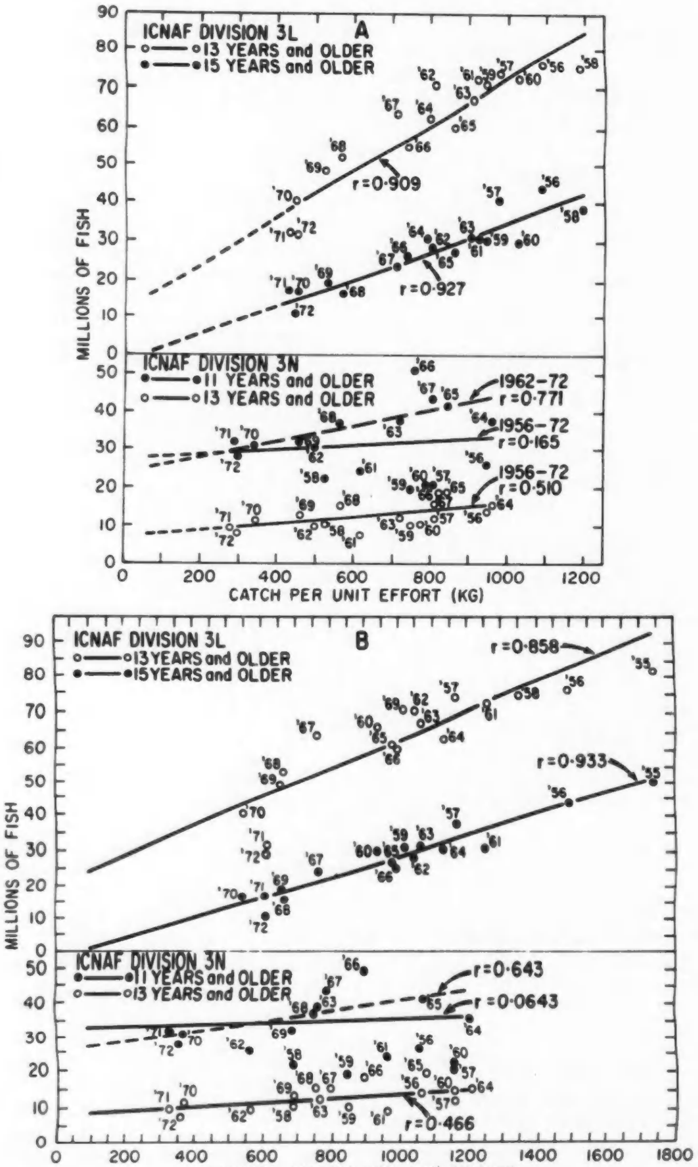


FIG. 5. A relation between A) catch per hour (weight) and stock abundance and B) catch per hour (numbers) and stock abundance.

or 12) of the von Bertalanffy growth curve indicated no significant difference between the slopes (rate of growth). In all cases, however, there was a significant difference between adjusted means (elevation). The similarity between rates of growth for different pairs of year-classes would appear to indicate that the initial growth period was probably critical in establishing the size at

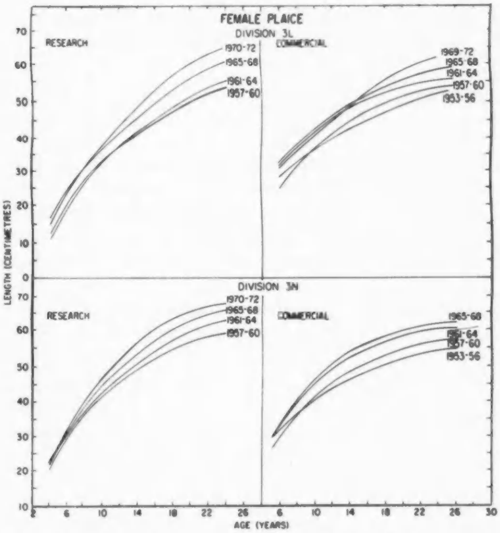


FIG. 6. Growth curve of female plaice for research and commercial data for ICNAF Divisions 3L and 3N.

age, and beyond this period there was not a great deal of difference in annual growth increments. Unfortunately, insufficient fish below age 4 were sampled to give a good idea of what happens during the early growth period.

The average size of plaice of various age-groups has also increased over the 14-yr span (1959–72) for which data were available (Fig. 8). In all cases, significant positive correlations were found in the plot of average size on a time scale. In some cases, however, standard errors of the estimates of the line of best fit were fairly large. The upward trend nevertheless was quite apparent.

Age and Length at Sexual Maturity

The age at 50% maturity in 1969–72 was significantly lower than in the earlier period in both ICNAF Divisions (Table 3). In Division 3L the age at M_{50} for the males changed from 7.59 ± 0.23 in 1961–65 to 6.43 ± 0.13 in the recent data and a corresponding change from 13.98 ± 0.23 to 10.57 ± 0.18 for the females. In Division 3N the decline was from 5.32 ± 0.13 to 4.65 ± 0.07 for males and 11.07 ± 0.15 to 8.79 ± 0.07 for the females. P was <0.001 in all cases.

There was no significant difference between the lengths at which male plaice were 50% mature for the two periods in each area ($P=0.30$ for Division 3L and 0.06 for Division 3N) (Table 3). Actually, for both periods and areas there was little difference in size at sexual maturity. For the females there was also no significant difference between the size at M_{50} for the two periods and areas ($P=0.30$ for Division 3L and 0.10 for 3N).

TABLE 2. Parameters of growth curves in Fig. 9. Values in brackets are standard errors.

Period	K	L_∞	to
		Commercial Div. 3L	
1953–56	0.088 (0.018)	59.413 (2.424)	−0.690 (1.783)
1957–60	0.127 (0.014)	57.014 (1.233)	1.579 (0.689)
1961–64	0.125 (0.023)	58.613 (2.094)	−0.235 (1.239)
1965–68	0.097 (0.018)	63.510 (3.022)	−0.504 (1.232)
1969–72	0.069 (0.021)	80.000 (3.122)	−0.541 (1.212)
		Commercial Div. 3N	
1953–56	0.090 (0.017)	59.533 (2.087)	−2.250 (1.341)
1957–60	0.124 (0.014)	60.711 (1.647)	0.166 (0.656)
1961–64	0.138 (0.011)	62.974 (1.427)	0.251 (0.370)
1965–68	0.135 (0.011)	65.182 (1.465)	0.384 (0.314)
		Research Div. 3L	
1957–60	0.083 (0.004)	64.221 (1.361)	1.350 (0.113)
1961–64	0.084 (0.007)	65.900 (2.285)	1.781 (0.271)
1965–68	0.067 (0.009)	77.522 (5.369)	0.395 (0.317)
1969–72	0.076 (0.010)	80.200 (4.269)	1.351 (0.222)
		Research Div. 3N	
1957–60	0.108 (0.004)	64.189 (0.984)	0.389 (0.120)
1961–64	0.093 (0.004)	70.385 (1.057)	−0.018 (0.116)
1965–68	0.099 (0.007)	72.938 (2.178)	0.404 (0.167)
1969–72	0.125 (0.009)	72.520 (1.832)	1.456 (0.111)

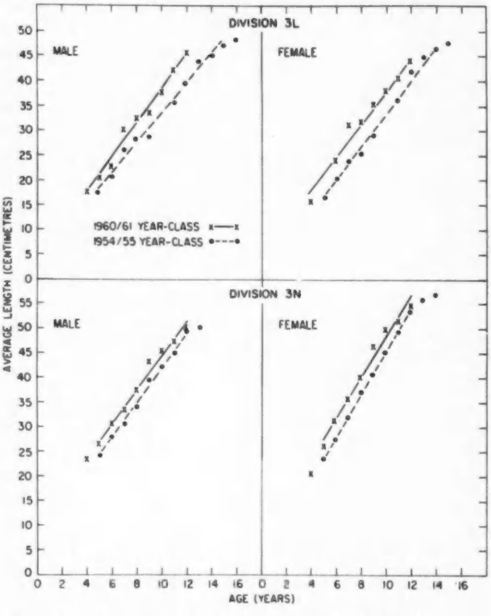


FIG. 7. Growth of 1954–55 and 1960–61 year-classes.

Changes in Length Related to Stock Size

In relating length at age to stock abundance significant correlations were found between L_∞ and stock size for both commercial and research data ($P=0.04$ and 0.05, respectively) from Division 3L (Fig. 9 and 10). For the other relation from 3L, significant correlations were found for the average size at age 5 and 10 for the research data and for age 10 of the commercial data (omitting 1969–72 data) ($P=0.05$ in all cases). For Division 3N no significant correlations were found, probably attributable to the somewhat erratic nature of the stock abundance estimates.

Trends in Water Temperature on the Grand Bank and Possible Relation to Differences in Size at Age

TEMPERATURE TRENDS

To document possible environmental changes that may have influenced plaice stock in size in Divisions 3L and 3N a series of water temperature observations from selected stations considered to be representative of the two Divisions was used (Fig. 11).

Little change in mean bottom temperatures throughout the whole period is apparent (Station 27) (Fig. 11), although average temperatures for the last two periods were slightly higher than in the two previous ones. In the upper 25 m, except for relatively high average temperatures for 1969–72 no trend was evident. For the three other Stations, 30, 36, and 37A (Fig. 11), in Division 3L no real trends were evident either in average bottom temperature or for the upper layer. In Division 3N, except for relatively high average temperatures at the upper layer in 1969–72 possibly because of Gulf water incursions, no real trends were evident at the more southerly stations (Fig. 11). Average values for Divisions 3L and 3N indicating the probable temperature conditions for the different periods are as follows:

	Div. 3L		Div. 3N	
	(A)	(B)	(A)	(B)
1950–52	−0.74	7.65	0.69	11.00
1953–56	−0.30	7.26	1.42	10.51
1957–60	−0.24	7.91	0.72	10.75
1961–64	−0.16	7.00	0.75	8.85
1965–68	−0.41	8.29	1.64	10.56
1969–72	−0.16	8.30	1.15	11.42

(A) Bottom temp.
(B) Surface — 25 m

3L average of stations 27, 36, and 37A; 3N average of stations 30, 32 and 33 (Fig. 1).

TABLE 3. List of ages and lengths at 50% maturity for American plaice for ICNAF Divisions 3L and 3N showing comparison for two time periods.

		Male					Female				
		Age		Length			Age		Length		
Area	Year	M_{50}	$S\bar{x}$	From curve M_{50}	Calc. M_{50}	$S\bar{x}$	M_{50}	$S\bar{x}$	From curve M_{50}	Calc. M_{50}	$S\bar{x}$
ICNAF	1961–65	7.59	0.23	25.52	23.46	0.65	13.98	0.23	41.50	42.14	0.39
Div. 3L	1969–72	6.43	0.13	26.00	23.91	0.29	10.57	0.18	41.10	40.36	0.19
ICNAF	1957–64	5.32	0.13	25.49	23.97	0.48	11.07	0.15	43.71	43.31	0.38
Div. 3N	1971	4.65	0.07	25.30	25.58	0.66	8.79	0.07	42.80	41.45	0.86

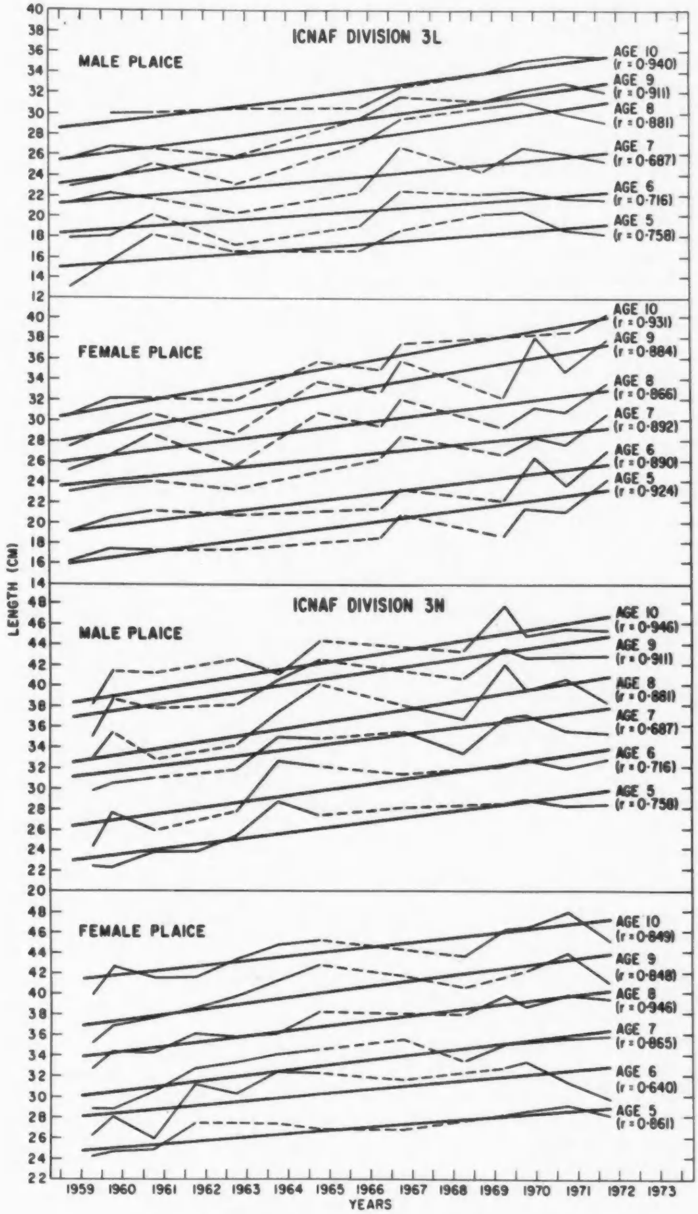


FIG. 8. Trends in growth of selected age-groups.

TEMPERATURE AND SIZE AT AGE

No significant correlations were found between average temperature and the various age-length parameters tested in the relation with stock abundance (Fig. 9 and 10). However, some positive trends were evident in Division 3L data and those giving the highest correlation coefficients are shown in Fig. 12. For commercial data asymptotic length (L_∞) on mean bottom tempera-

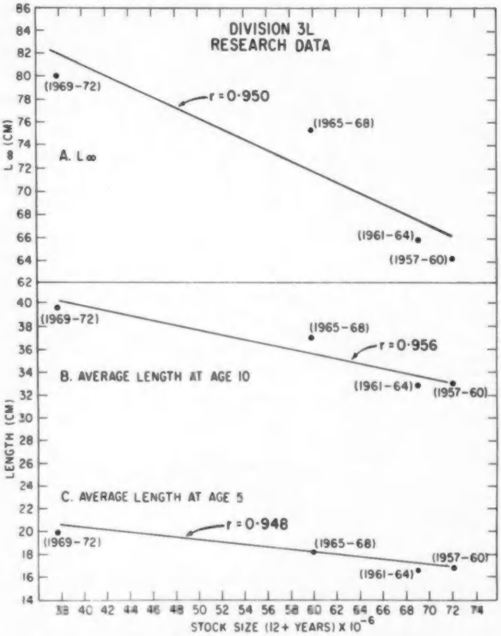


FIG. 9. Relation between stock abundance and asymptotic length (L_x) and average size at ages 5 and 10 yr for research data from Division 3L.

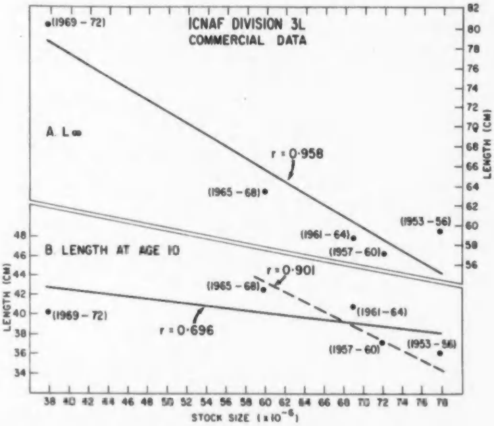


FIG. 10. Relation between stock abundance, asymptotic length, and average size at age 10 for commercial data from Division 3L.

ture of the previous period (i.e. L_∞ for 1953–56 on temperature for 1950–52) gave an r value of 0.848 (P=0.07) and a similar plot for research data gave r value of 0.768 (P>0.20) for L_∞ and 0.878 (P>0.10) for the age 10 fish. For other plots of Division 3L data r values were below 0.750. Correlations with average temperatures

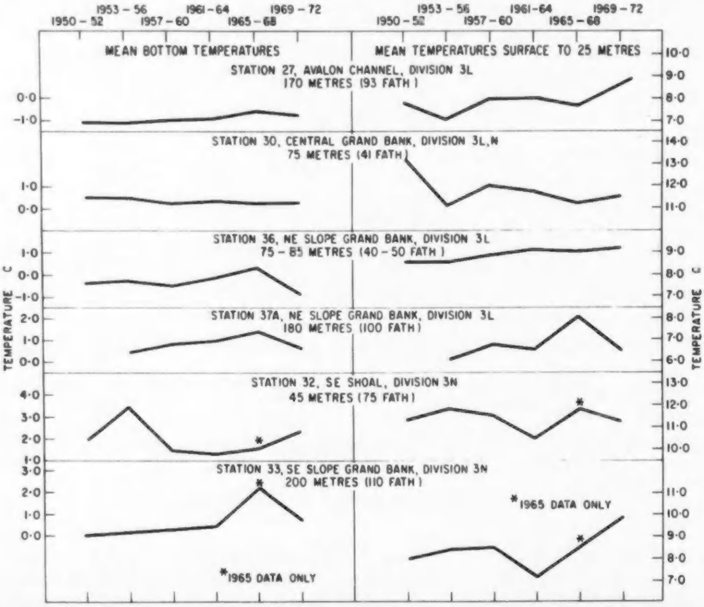


FIG. 11. Water temperatures from selected hydrographic stations for ICNAF Divisions 3L and 3N.

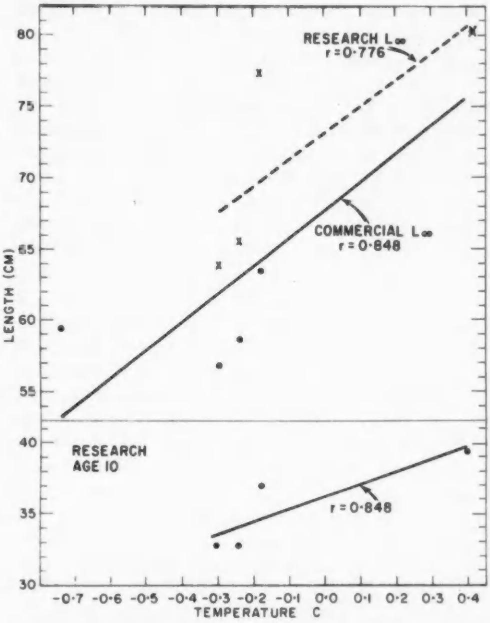


FIG. 12. Relation between mean bottom temperature and L_∞ and size at age 10 from Division 3L.

surface to 25 m gave approximately the same trends but with slightly lower coefficients. For Division 3N no significant correlations were found; in fact, negative trends were found with upper layer temperatures.

Discussion

CHANGES IN GROWTH AND ABUNDANCE

For Division 3L the evidence points to a gradual decline in abundance. Catch per unit effort both in weight and numbers and stock size estimates (Fig. 3 and 4) point to a downward trend. For Division 3N, however, the pattern appears to be somewhat different with an apparent increase in abundance during the mid-1960s. There was no evidence of a reduction in recruitment since it was previously shown (Pitt 1973) that for the younger ages there was, if anything, an increase in recruitment in recent years; although as indicated, stock estimations here may have considerable error because of discards of small fish. The main fishing effort by the Newfoundland based fleet up to 1962 was for haddock with the primary effort in Division 3N. The decline in haddock abundance resulted in a diversion of effort to plaice at this time, and coincident with the decline of haddock was the introduction, in 1964, of the more efficient stern trawler and the directed effort for plaice increased with the fleet concentrating on localities previously either fished lightly or not at all. During the mid-1960s in Division 3N then, the concentration of directed effort moved from southern localities to more northern locations on the eastern slope near 45° N lat. (Fig. 1).

While the increase in catch per hour in Division 3N may have been the result of an increase in fishing efficiency and a change in location to previously lightly fished concentrations, the possibility of an increase in abundance should not be overlooked. If there was an increase in abundance because of strong year-class survival, this should be reflected in the catch per hour of fish that are fully recruited to the fishery and are making a major contribution to the total numbers caught. In neither Division was there any evidence of an increase in abundance of these age-groups (Fig. 3B). In Division 3N the total catch per hour of fish 11 yr and older does not indicate an increase in abundance that might be suggested from the catch per unit effort data and from stock estimations. This, coupled with the fact that there was poor correlation between stock size and catch per unit effort for data prior to 1963 (Fig. 5) for this Division, would indicate that up to about 1963 the total population in Division 3N was incompletely sampled because fishing was largely limited to a portion only of this Division.

In Division 3L, however, excellent correlations were found between stock size and the catch per unit effort. The fishery here by the Canadian deep sea fleet has been almost exclusively for plaice with effort generally spread throughout the Division probably resulting in a good sampling of the population.

Within the whole northwest Atlantic there is a fairly high degree of variability in the size at age of plaice. In a previous paper, Pitt (1967) showed that female plaice collected in research cruises varied significantly in size at age for a number of localities sampled. A positive association was found between size at ages 5 and 15 for the various localities and the probable bottom temperature (Pitt 1967).

The evidence present here indicates a gradual increase in size at age during the period under consideration. Growth curves (Fig. 7) show a consistent increase in elevation although the standard errors (Table 2) of the various parameter suggest that some of the curves would overlap if the upper and lower values were put into the equation. Trends, however, are quite evident and coupled with the evidence from age-groups and year-classes (Fig. 7 and 8) confirm the fact that an increase in growth has occurred.

Growth of fish depends ultimately upon the availability and utilization of food. Environmental conditions such as temperature control the utilization of food, but as McKenzie (1934, 1935) and Kohler (1964) indicated for cod, temperature was related to growth indirectly inasmuch as it controlled the food supply. The previously mentioned association between average size at age and temperature for a number of geographic regions (Pitt 1967) suggests that temperature conditions controls ultimate fish size probably by its influence on the availability of prey species both in quantity and type.

Available hydrographic data (Fig. 11) suggest a fairly stable temperature regime within the two Divisions during the period considered here. No significant correlations were found between temperature and various age-length parameters. However, certain positive trends suggesting an increase in size at age with temperature were observed in Division 3L. The difficulty with temperature information used with so few data points is that anomalous conditions in one or two adjacent years can mask a general trend. The latter is particularly applicable to Division 3N where incursions of Gulf Stream water produce abnormal conditions in certain years. It is therefore suggested that changes in size at age may be to a large extent the result of a reduction in the density of plaice or other competing species. The evidence for Division 3L was particularly strong with significant correlations between size and stock abundance (Fig. 9 and 10); however, some caution should be exercised in putting much credence in the relation with asymptotic length (L_∞) since it may be susceptible to change depending upon the range of ages used in fitting the curve.

While there is no evidence that stock density per se influenced rate of growth of plaice on the Grand Bank, there is information in the literature indicating that crowding may affect the feeding of fish; thus Brown (1957) showed that *Salmo trutta* fry did not feed well in the presence of larger fish and that overcrowded fish ate less and utilized food less efficiently than fish in less crowded conditions. However, Kohler (1964) found that food supply was the main factor influencing growth. Sonina (1965) stated that while factors such as temperature and other conditions of the sea may exert an influence on growth, the primary cause of an increase in growth of Barents Sea haddock was a reduction in abundance and May (1966) indicated a similar condition for Labrador cod.

Not only were plaice reduced in numbers, but also competitors such as cod and haddock have been heavily exploited thus changing various interspecific relationships. Capelin and lance are major food items for plaice (Pitt 1973b) and a reduction in cod density would be expected to increase the abundance of these two prey species.

For American plaice below 30 cm, the greatest percentage of total food (weight) was crustaceans, principally amphipods and cumaceans, followed closely by small brittle stars (*Ophiuroidea*), and other echinoderms (Pitt 1973b). Above 30-cm fish, principally lance and capelin accounted for the greatest proportion of the total diet, although in Division 3L echinoderms are still a major item and are still competitors with the smaller fish. The difference in average size at age beyond the first 4 or 5 yr is not all that large and no significant difference was found between the rate of growth (slopes) for the 1954–55 and 1960–61 year-classes (Fig. 8). Elevation (size at age) apparently was determined at a fairly early age when plaice were feeding mainly on crustaceans and other small bottom forms. Obviously with a limit on the particle size that can be taken, the density of the prey animals is important with competition from both large and small plaice and from other bottom feeders. Yanulov (1962) attributed the slow growth of plaice on the northern half of the Grand Bank (Division 3L) to high abundance and an inadequate food supply.

SIZE AND AGE AT SEXUAL MATURITY

The apparent increase in size at age over a 6- or 7-yr period resulted in a significant reduction in the time required to attain sexual maturity. This suggests that gonad development is a function of body size with hormones that initiate sexual maturity being produced only when the fish and hence the gonads have reached a certain size or level of development. However, in spite of this, Pitt (1966) found that plaice from the southwest slope of the Grand Bank (mostly Division 30), although they were larger at comparable age, matured at a greater age than those from slower-growing localities. Plaice from Flemish Cap (Division 3M), which had by far the largest size at age (Pitt 1967), matured at significantly lower ages than those from any other locality (Pitt 1966). Fleming (1960) also showed that although Labrador cod had the slowest rate of growth for the entire Newfoundland–Labrador area, they matured at a lower age.

The relation between fish size and the attainment of sexual maturity is not entirely clear. However, Alm (1959), in a summarization of the literature and of his own experimental work, states that for any particular species, stock or population that in the beginning exhibits a good rate of growth generally reaches sexual maturity at an earlier age than a stock with a slower initial growth rate. He also pointed out, however, that age of sexual maturity could be genetically determined, thus explaining the early maturation of small fish in certain species. Karlander (1932) observed that when a heavy fishery drastically reduced the population size of the flounder (*Pleuronectes flesus*) in the Baltic, an acceleration in growth and a reduced age at sexual maturity by 1 yr occurred. Gross (1949) with the same species reported that the fertilization of a sea lock improved feeding conditions, increased growth, and also lowered age at sexual maturity. As previously noted, the major change in size at age in Grand Bank plaice appeared to be in the initial years and this could trigger an early maturation.

Acknowledgments

I am especially indebted to Mr C. A. Rose and Mr C. Butt for the determination of the age of the fish and in the preparation of the data for publication. I also acknowledge the assistance of other members of the technical and scientific staff who assisted in the collection of the data and to Mr A. T. Pinhorn who made many helpful suggestions in the preparation of the manuscript.

ALLEN, K. R. 1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board Can. 23: 163–179.

ALM, G. 1959. Connection between maturity, size and age in fishes. Rep. Inst. Freshwater Res. Drottningholm 40: 145 p.

ANON. 1974. Revised nominal catches of flounder by species, country and division, 1963–72. Intern. Comm. Northwest Atl. Sum. Doc. 74/34, Ser. No. 3317.

BARANOV, F. I. 1918. On the question of the biological basis of fisheries. Nauchn. issled. ikithiologich-eskii Inst. Isvest. 1(1): 81–128. (In Russian)

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Min. Agr. Fish. Food Fish Invest. (2)19: 533 p.

BLISS, C. I. 1935a. The calculation of dosage-mortality curve. Ann. Appl. Biol. 22: 134–167.

1935b. The comparison of dosage mortality data. Ann. Appl. Biol. 22: 307–333.

1952. The statistics of bioassay with special reference to the vitamins. Academic Press Inc., New York, N.Y. 184 p.

BROWN, M. E. 1957. Experimental studies on growth. *In* The physiology of fishes. Vol. 1. Academic Press Inc., New York, N.Y. 447 p.

FLEMING, A. M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area 1947–50. J. Fish. Res. Board Can. 17: 775–890.

FRY, F. E. J. 1949. Statistics of lake trout fishery. Biometrics 5: 26–67. 1957. Assessment of mortalities by use of virtual populations. Proc. Joint Scientific Meeting ICNAF, ICES, and FAO on fishing effort and effects of fishing on resources and selectivity in fishing gear. Contr. No. P15. (Mimeo)

GROSS, F. 1949. Further observations on fish growth in a fertilized sea loch (Loch Craiglin). J. Mar. Biol. Ass. U.K. 28: 1–19.

GROSSLEIN, M. D., AND A. T. PINHORN. 1971. Progress in development of co-ordinated survey program in the ICNAF area. Intern. Comm. Northwest Atl. Fish. Res. Doc. 71/128, Ser. No. 2634. (Mimeo)

GULLAND, J. A. 1955. Estimation of growth and mortality in commercial fish populations. U.K. Min. Agr. Fish. Invest., Ser. 2, 18(9).

1965. Estimates of mortality rates. Annex to Arctic fisheries working group report. Int. Comm. Explor. Sea. CM 1965 Doc. 3. (Mimeo)

JONES, R. 1968. Appendix to Report of the northwest working group. Int. Comm. Explor. Sea. CM 1968 Doc. 20. (Mimeo)

KARLANDER, R. 1932. Veränderungen im flundernliestand der Ostsee durch die fisherei. Cons. Int. Explor. Mer. Rapp. Proc. Verb. 78(3): 1–45.

KOHLER, A. C. 1964. Variations in the growth of Atlantic cod (*Gadus morhua* L.). J. Fish. Res. Board Can. 21: 57–100.

MAY, A. W. 1966. Biology and fishery of Atlantic cod (*Gadus morhua morhua* L.) from Labrador. Ph.D. Thesis. McGill University. Montreal, Que. 225 p.

MCKENZIE, R. A. 1934. Cod and water temperature. Biol. Board Can. Atl. Progr. Rep. 12: 3–6.

1935. Codfish in captivity. Bio. Board Can. Atl. Progr. Rep. 16: 7–10.

PALOHEIMO, J. E. 1961. Studies of estimation of mortalities. I. Comparisons of a method described by Beverton and Holt and a new linear formula. J. Fish. Res. Board Can. 18: 645–662.

PITT, T. K. 1961. Vertebral numbers of American plaice, *Hippoglossoides platessoides* (Fabricius), in the Northwest Atlantic. J. Fish. Res. Board Can. 20: 1159–1181.

1966. Sexual maturity and spawning of American plaice, *Hippoglossoides platessoides* (Fabricius), from Newfoundland and Grand Bank areas. J. Fish. Res. Board Can. 23: 651–672.

1967. Age and growth of American plaice (*Hippoglossoides platessoides*) in the Newfoundland area of the Northwest Atlantic. J. Fish. Res. Board Can. 24: 1077–1099.

1969. Migrations of American plaice on the Grand Bank and in St. Mary's Bay, 1954, 1959, and 1961. J. Fish. Res. Board Can. 26: 1301–1319.

1973a. Assessment of American plaice stocks on the Grand Bank, ICNAF Divisions 3L and 3N. Int. Comm. Northwest Atl. Res. Bull. 10: 63–77.

1973b. Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. J. Fish. Res. Board Can. 30: 1261–1273.

RICKER, W. E. 1948. Methods of estimating vital statistics of fish populations. Indiana Univ. Publ. Sci. 15.

SCHUMACHER, A. 1970. Bestimmung der fishereilichen Sterblichkeit beim Kabeljaubestand vor West Grönland. Ber. Dtsch. Komm. Meeresforch 21(1–4): 248–259 Transl. from German by Fish. Res. Board Can. Transl. Ser. No. 1690, 1900)

SONINA, M. A. 1964. Relationship between the growth rate and population density of haddock in the Barents Sea. Int. Comm. Northwest Atl. Fish. Spec. Pub. 6: 565–570.

YANULOV, K. P. 1962. Age and growth of American plaice in the Northwest Atlantic. Soviet fisheries investigations in the Northwest Atlantic. VINRO–PINRO. Transl. from Russian, U.S. Rep. Int. Natur. Sci. Found. Off. Tech. Ser. 63–11102: 355–360.

Sedimentation of Organic Matter in St. Margaret's Bay, Nova Scotia[1]

T. J. M. Webster, Madhu A. Paranjape[2]
Department of the Environment, Fisheries and Marine Service, Marine Ecology Laboratory, Bedford Institute of Oceanography, Dartmouth, N.S. B2Y 4A2

and K. H. Mann

Department of Biology, Dalhousie University, Halifax, N.S.

Webster, T. J. M., M. A. Paranjape, and K. H. Mann. 1975. Sedimentation of organic matter in St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 32: 1399–1407.

Sediment traps were placed at two sites in St. Margaret's Bay. At a deep station (70 m), traps were placed 5 m and 10 m above the bottom; at a shallow station (10 m), six traps were placed between 45 and 197 cm above the bottom. Total catch averaged 118 g C m^{-2}yr^{-1} at the deep station and 134 g C m^{-2}yr^{-1} at the shallow station. The most probable source of the organic matter was detritus derived from seaweeds and seagrasses, but the most probable source of inorganic material was bottom sediment. It is suggested that the traps were taking bottom sediment resuspended from shallow water, enriched by detritus from seaweeds and seagrasses.

Webster, T. J. M., M. A. Paranjape, and K. H. Mann. 1975. Sedimentation of organic matter in St. Margaret's Bay, Nova Scotia. J. Fish. Res. Board Can. 32: 1399–1407.

Nous avons placé des trappes à sédiment à deux endroits de la baie St. Margaret. A une station profonde (70 m), les trappes ont été placées à 5 et 10 m au-dessus du fond; à une station peu profonde (10 m), nous avons placé six trappes à 45–197 cm au-dessus du fond. La prise totale a été de 118 g C m^{-2}an^{-1} en moyenne à la station profonde et 134 g C m^{-2}an^{-1} à la station peu profonde. La source la plus probable de matière organique sont des détritus dérivés des varechs et herbes marines, mais la source la plus probable de matière organique est le sédiment du fond. Nous suggérons que les trappes capturent le sédiment du fond resuspendu de l'eau peu profonde et enrichi des détritus de varechs et d'herbes marines.

Received August 15, 1974
Accepted March 18, 1975

Reçu le 15 août 1974
Accepté le 18 mars 1975

Prediction of the sustainable yield of bottom living fish on different areas of the seafloor could be made with more confidence if we had more knowledge of the dynamics of benthic food chains. There is a great deal of information on the biomasses of benthic invertebrates constituting the food of fishes, and some information on benthic productivity (e.g. Sanders 1956; Richards and Riley 1967; Peer 1970; Burke and Mann 1974). However, information on the level of food input to benthic communities and of benthic food/growth efficiencies is very sparse indeed. Riley (1956) estimated that in Long Island Sound, where primary production was of the order of 200 g C m^{-2} yr^{-1} about two thirds was consumed by the plankton, leaving 60–70 g C m^{-2} yr^{-1} for the benthos. In the Sargasso Sea, he estimated that only 2–3 g C m^{-2} yr^{-1} reached the benthos (Riley 1970). Stephens et al. (1967), using sediment traps placed 2 m from the bottom at a station 30 m deep off the coast of Vancouver Island, collected about 200 g C m^{-2} yr^{-1}, but estimated that about half the material was of terrestrial origin carried by river runoff. In the Baltic, a trap 1 m above the bottom at a site 25 m deep collected 40 g C m^{-2} yr^{-1}, an unknown proportion of which was resuspended bottom material (Zeitzschel 1965). In a Scottish sea loch, Steele and Baird (1972) were able to distinguish phytoplankton and sinking zooplankton feces from resuspended bottom material, and concluded that the input of new organic matter to the bottom was about 30 g C m^{-2} yr^{-1}.

This paper reports studies of the input of organic matter to the benthos at two sites in St. Margaret's Bay, Nova Scotia. Other studies in the bay have given information on phytoplankton production (Platt 1971), seaweed production (Mann 1972a), and the annual cycle of production and decay in eelgrass (Harrison and Mann 1975).

---

[1] Bedford Institute of Oceanography Contribution.

[2] All correspondence should be addressed to M.A.P.

Printed in Canada (J3526)
Imprimé au Canada (J3526)

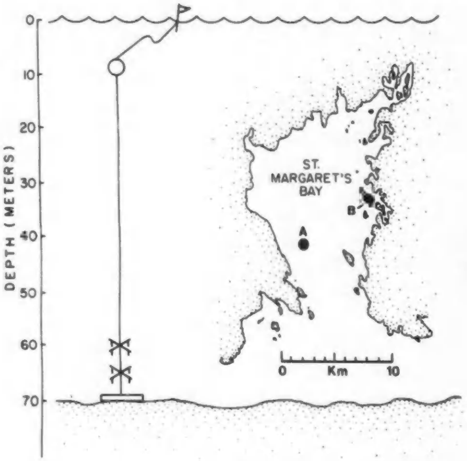


FIG. 1. Arrangements for sampling at the deep station. Inset — St. Margaret's Bay showing deep station (A) and shallow station (B).

Methods

DEEPWATER STATION

Sediment traps were placed at depths of 60 m and 65 m at a station (A in Fig. 1; position 44° 30.4′N, 64°00.2′W) where the water is 70 m deep. The traps consisted of polyvinyl chloride tubes 31 cm tall and 7.5 cm internal diameter, closed at the bottom but open at the top. Four tubes were clamped in a metal bracket at each depth, on a vertical wire held in position by a heavy anchor and a subsurface float (Fig. 1). As a check on loss of sediment, one of the PVC tubes was occasionally replaced by a tube of clear acrylic plastic, in which it was observed that when the samples were hauled on board ship a discrete and undisturbed layer of sediment was always present. The maximum coefficient of variation for total sediment weight was 26%, while the minimum was 2%. For organic carbon the range of variation was 17–2 %.

In the laboratory, the contents of each sediment tube were thoroughly mixed, and subsamples were withdrawn for measuring total plant pigments, organic carbon, and organic nitrogen. Aliquots for pigment were filtered through a 5.5-cm Whatman Gf/C filter and were analyzed by the fluorometric method of Yentsch and Menzel (1963) as modified by Holm-Hansen et al. (1965). Organic carbon and nitrogen aliquots were filtered through prebaked Selas Flotronics Silver Filters (0.8 μm) and were analyzed with an F & M Model 185 C-H-N analyzer. Contents of two of the tubes were used to estimate total sediment weight and combustible organic matter, by settling, centrifuging, desalting, and freeze-drying the sample, and weighing before and after ignition at 450 C. The contents of the other two tubes were washed on a 53-μm sieve and preserved in ethanol for microscopic examination. The traps were position from July 1970 to July 1971.

SHALLOW-WATER STATION

Six traps were placed between Mosher Island and Troop Island (B in Fig. 1; position 44°35.2′N, 63° 56.0′W) at a point where the water is 10 m deep. The traps were similar to those used at the deep station, but 25 cm tall and 7.0 cm internal diameter. Each trap was attached separately to a steel rod driven into the seabed, and the mouths of the traps were 49, 96, 127, 152, 183, and 197 cm from the bottom. In addition, two large traps of 37.5 cm diameter, 42 cm deep, were placed with their mouths 115 and 146 cm from the seafloor, to catch larger quantities of sediment for chemical analysis. Traps were serviced by SCUBA divers, who capped them, replaced them by empty traps, and brought them to the surface. To minimize the risk of significant loss by decay, these traps were visited every 2 wk. Contents of the small traps were filtered on 0.45-μm Millipore filters, dried at 65 C, and weighed. Contents of the large traps were settled, centrifuged, desalted, and analyzed for organic carbon and nitrogen, as described for the deepwater samples. The traps were in position from May 1971 to May 1972.

OTHER OBSERVATIONS

Organic content was determined by the wet oxidation method of Walkley (1947) on 18 samples from the shallow-water traps, 11 samples from the seafloor near the deep traps, and 10 samples from the seafloor near the shallow traps.

Rainfall was measured at a site 12.8 km from the shallow station (44°42′N, 63°54′W). The duration of the spring phytoplankton bloom in 1972 was monitored by following the chlorophyll and pheophytin content of the water column, using the methods of Lorenzen (1965).

Results

Catch of sediment at the deepwater station (Fig. 2) varied from about 2–8 g m^{-2} day^{-1}. Of this, the organic matter content was 15–20%, and organic carbon sedimentation in the range 0.1–0.5 g C m^{-2} day^{-1}. The organic matter content is a little high as compared with the carbon values. A possible source of error, since organic matter was determined by weight loss in combustion, is the inclusion of small amounts of hygroscopic, molecularly bound water in the dried sediments. Rates were consistently higher at 65 m than 60 m, and highest values were observed in the first 4 mo of the year, with a peak in February. Summer values were low. The total sediment catch for the year was 1685 g m^{-2} yr^{-1}, of which 118 g (nearly 7%) was carbon and

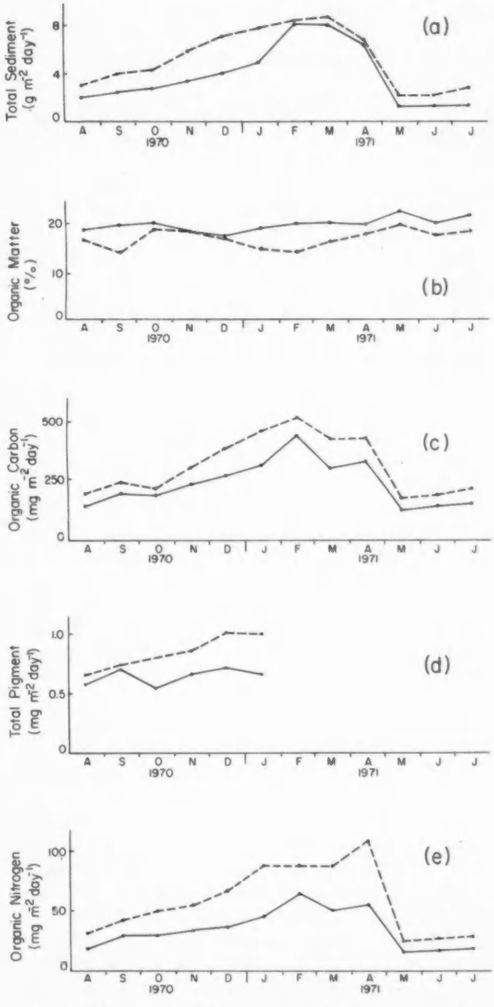


FIG. 2. Rates of sedimentation at the deep station, showing (a) total sediment, (b) percent organic matter, (c) organic carbon, (d) total pigment, and (e) organic nitrogen. ———, 60 m; -------, 65 m.

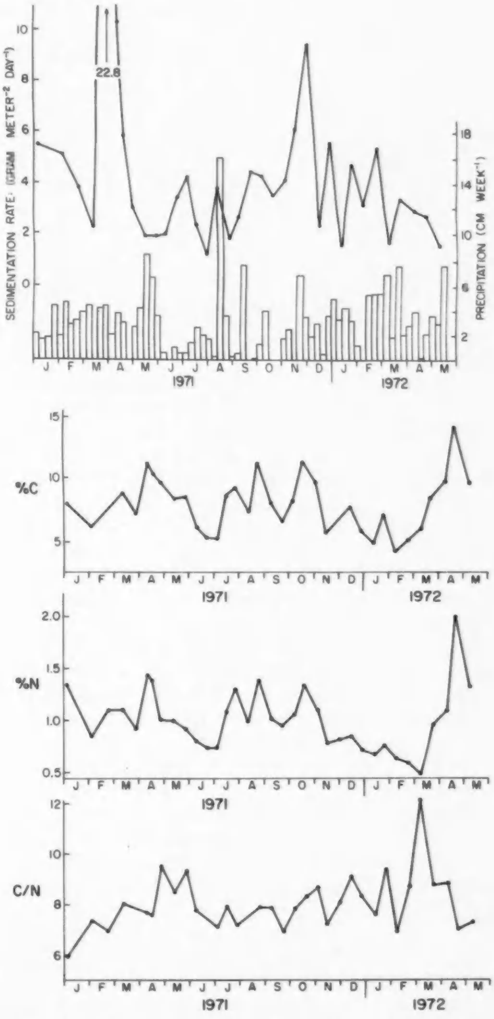


FIG. 3. *Above*, rates of sedimentation at the shallow station, and precipitation at a nearby meteorological station; *below*, analysis of sediments collected at the shallow station in terms of percentage carbon, percentage nitrogen and carbon:nitrogen ratio.

17 g (about 1%) was nitrogen. The series of data on total plant pigment in the sediments is incomplete, as some samples were accidentally destroyed.

At the shallow station the rate of sedimentation was about the same as at the deep station, mostly in the range 2–6 g m^{-2} day^{-1}. Average rate of catch in the lowest trap (25.7 mg day^{-1}) was 25% higher than in any other, so the data were discarded on the assumption that it was catching resuspended bottom material. The catch from the other five traps average 18.0 mg day^{-1}, 1706 g m^{-2} yr^{-1} or 134 g C m^{-2} yr^{-1} (Table 1). Seasonal variation in the rate of catch is shown in Fig. 3, with peaks occurring in April and November of 1971. However, the spring peak was not repeated in 1972. As at the deep station, the organic carbon content was usually in the range 5–8%, with a few samples having more than

TABLE 1. Dry weight of sediment in traps at the shallow station at various heights above bottom, and their carbon equivalents.

Trap height above bottom (*cm*)	No. samples	Days of trapping	Mean daily catch (mg dry wt)	Total catch g m^{-2} yr^{-1}	Carbon equivalent g C m^{-2} yr^{-1}
197	26	355	16.4±16.4	1556	121
183	20	258	20.5±19.9	1945	159
152	26	355	17.9±16.4	1699	134
127	24	322	15.4±9.5	1461	110
96	24	330	19.7±17.4	1870	146
49	25	341	25.7±21.6	2439	181
Mean, excluding lowest trap			18.0±2.1	1706±204	134±20

10% (Fig. 3). Carbon:nitrogen ratios were usually near to 8:1. Organic matter as determined by the wet oxidation method gave the following results: from the shallow-water traps, 10.77 ± 2.69%; from the seabed near these traps, 4.52 ± 0.92% from the seabed near the deep traps, 6.56 ± 0.21% organic matter.

Microscopic examination of the sieved trap contents from deep water showed a variety of recognizable plant and animal remains. These included diatoms, dinoflagellates, tintinnids, foraminifera, cladoceran carcasses and resting eggs, copepod carcasses and eggs, crustacean appendages, egg capsules of *Littorina* sp., gastropod larval shells, bivalve larval shells, and empty shells of *Spiratella retroversa*. Cumaceans, amphipods, and harpacticoid copepods occurred in small numbers, together with a few polychaete and echinoderm larvae. Flocs of material, consisting of fine silt, sand, amorphous organic matter, and fecal pellets of various sizes were found in large quantities. Apart from a few pollen grains and wood fibers, almost nothing of terrestrial origin was recognized.

Settlement rates of various kinds of animal remains in the deepwater traps are shown in Fig. 4. Resting eggs of Cladocera were abundant in summer and fall; eggs of *Tortanus discaudatus* were common in late summer and in winter; bivalve larvae and pelagic foraminifera were abundant in late fall, while empty shells of *Spiratella retroversa* showed peak settlement in early winter. As expected, the arrival of this "debris" in the sediment corresponds with the seasonal abundance of these organisms in the water column (Paranjape and Conover 1973).

Microscopic examination of trapped material from shallow water showed large quantities of amorphous organic matter acting as a binder for sand grains, fecal pellets, pollen grains, wood, and other plant fibers. During the spring phytoplankton bloom, recognizable cells of *Chaetoceros*, *Thalassiosira*, *Pleurosigma*, *Skeletonema*, and *Tintinnopsis* were present. Very few remains of planktonic animals were seen.

Interpretation of Results

The observed sedimentation rate of organic carbon is 118 and 134 g C m^{-2} yr^{-1} at the deep and shallow station, respectively. The key question is: are the figures truly representative of transfer of organic carbon from the water column to the sediments, or are they distorted by inclusion of significant amounts of resuspended sediment? This question can be examined in the light of what is known about events in the water column.

Seasonal cycles of temperature, salinity, total pigment (chlorophyll *a* + pheophytin), primary production, and zooplankton biomass are shown in Fig. 5. Total pigment and primary production values are taken from a 3-yr study by Platt and Irwin (1970). Zooplankton data are from a 3-yr study by Paranjape and Conover (1973). Hydrographic conditions in St. Margaret's Bay are characterized by strong gradients of temperature and salinity during summer and fall, while in winter and early spring the water column is well mixed. In April, stabilization of the water column initiates an intense spring bloom of phytoplankton while the renewal of surface nutrients in the fall leads to a smaller bloom. Hence, the seasonal cycle of primary productivity is fairly typical of temperate, coastal waters. Zooplankton, numerically dominated by small copepods through most of the year, shows peak abundance in summer and fall.

ROLE OF PHYTOPLANKTON

The deposition of organic carbon in the traps reached a peak in February, well before the spring bloom of phytoplankton. Moreover, over the period for which data are available, the quantity of plant pigment in the traps amounted to only 4% of that present in the water column

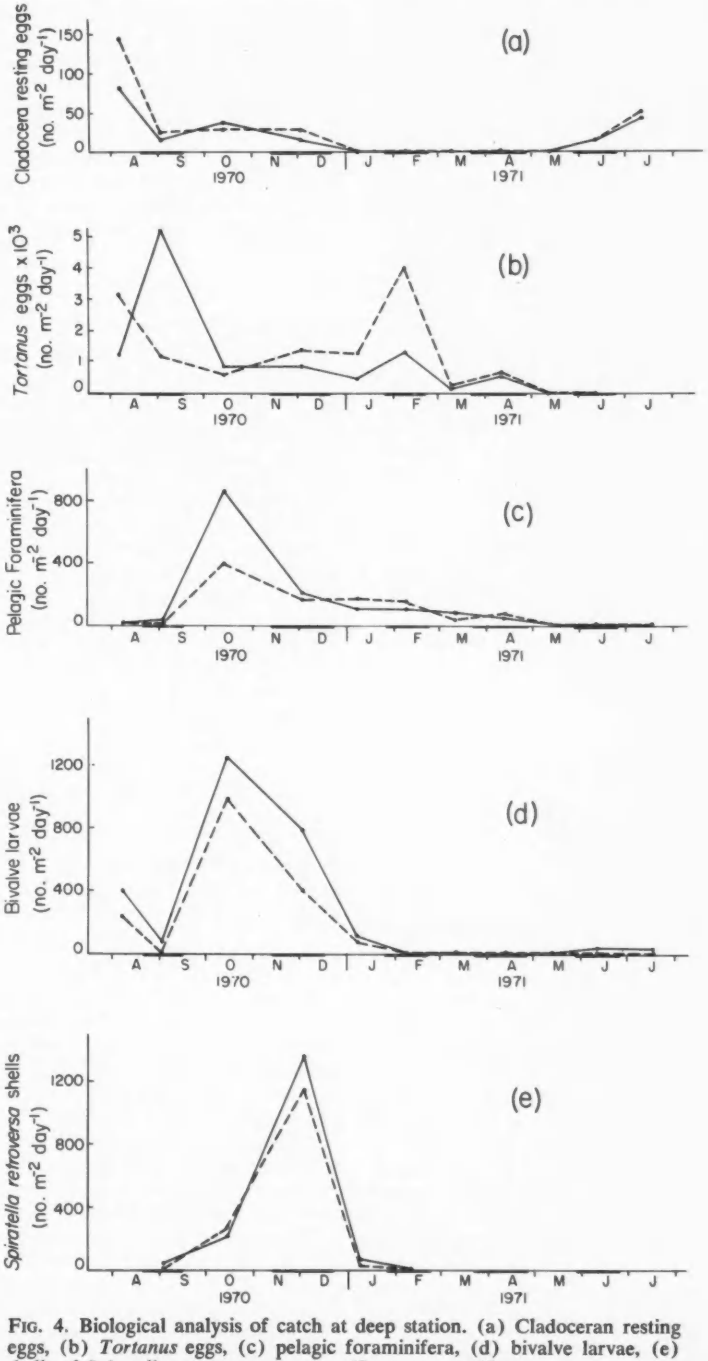


FIG. 4. Biological analysis of catch at deep station. (a) Cladoceran resting eggs, (b) *Tortanus* eggs, (c) pelagic foraminifera, (d) bivalve larvae, (e) shells of *Spiratella retroversa*. ———, 60 m; -------, 65 m.

TABLE 2. Spring chlorophyll:pheophytin ratios at the shallow station.

Date	Depth	Ratio chlorophyll:pheophytin
Mar. 30, 1972	3.0 m	2.794
	4.5 m	2.906
Apr. 7, 1972	3.5 m	2.733
	3.5 m	2.500
Apr. 18, 1972	3.5 m	1.754
	3.5 m	1.214
Apr. 29, 1972	3.5 m	0.133
	3.5 m	0.333

above. Hence, it seems unlikely that the observed sedimentation of organic matter is derived primarily from sinking of phytoplankton. On the other hand, the pattern of occurrences of animal remains coincides closely with what is known of their life histories in the plankton. It seems probable that most of the phytoplankton is consumed by the zooplankton, and that the resulting rain of organic detritus is composed mainly of fecal pellets and animal fragments.

At the shallow station in 1972, the chlorophyll: pheophytin ratio was monitored in late March and early April, as an index of the progress of the spring bloom of phytoplankton (Table 2). During the bloom, there was a marked increase in carbon and nitrogen content of the material trapped at the shallow site, but the total dry weight of the material was not high. However, during the spring bloom of the previous year, April 1971, there had been a very large increase in weight of sediment, accompanied by only a slight increase in carbon and nitrogen content. Clearly, changes in rate of sedimentation at the shallow station are not a reflection of events in the phytoplankton.

ROLE OF LAND DRAINAGE

Rivers entering St. Margaret's Bay are small: the two largest are in the northwest and northeast corners (Fig. 1), neither of them close to the sampling stations. In 1970–71 high values of freshwater runoff occurred in August, February, April, and May. In August and May the catch of sediment at the deep station was particularly low, in February and April it was high. There does not appear to be any correlation between river runoff and sedimentation at the deep station.

The more detailed information from the shallow station was tested statistically to see if there

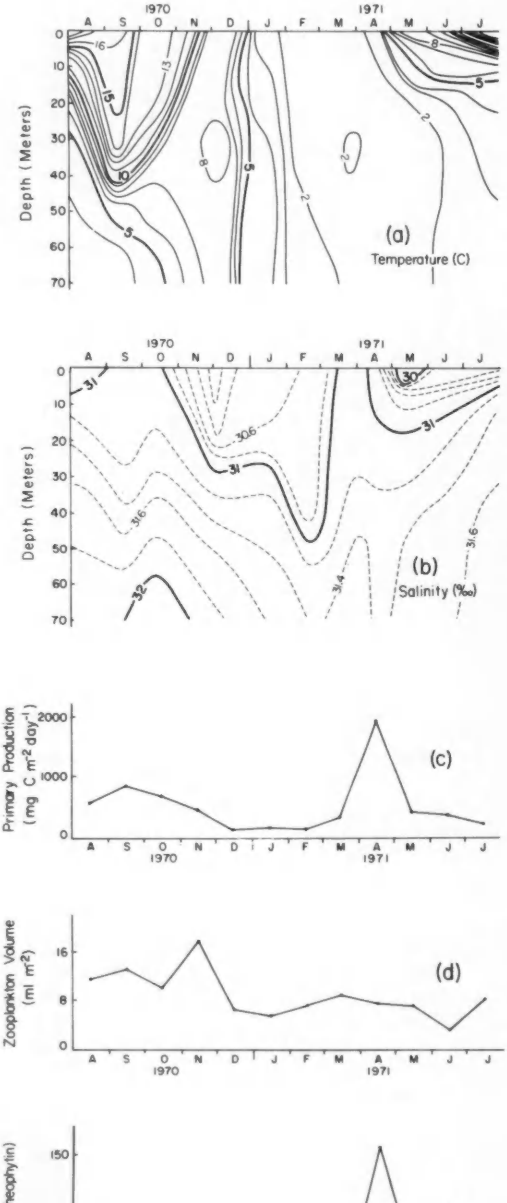


FIG. 5. Seasonal cycles in St. Margaret's Bay. (a) Temperature, (b) salinity, (c) primary production, (d) zooplankton volume, (e) total pigments.

were any correlations between weight of sediment and either (i) the rainfall of the week in which the samples were taken or (ii) the rainfall 2 wk earlier. In neither case was a significant correlation obtained. Inspection of Fig. 3 shows that the week with the highest rainfall, in August 1971, is associated with medium to low catches of sediment. Conversely, the peak of sedimentation rate in the spring of 1971 is associated with a long period when the rainfall was close to average.

ROLE OF MARINE MACROPHYTES

It has been shown (Mann 1972b) that averaged over the 138 km^2 of the bay surface, kelp (*Laminaria*) production in 1969–70 amounted to 3 times the production of phytoplankton. The peak growth rate in kelp is reached in late winter, before the spring bloom of phytoplankton. Winter storms lead to erosion of the blades, producing large amounts of particulate organic detritus. Sutcliffe (1972) also noted maximum amounts of nonliving particulate organic matter in suspension in the bay in late winter, and Hargrave (1973) found high rates of oxygen uptake in the sediments in late winter. The kelps are particularly abundant along the western shores of the bay, adjacent to the deepwater sampling station. Mann (1972b) estimated the annual production of seaweeds at 603 g C m^{-2} yr^{-1} and Platt (1971) gave a value of 190 g C m^{-2} yr^{-1} for the production of phytoplankton. So, the 118 g C m^{-2} yr^{-1} in the traps at the deep station amounts to about 15% of total plant production. The large seaweeds provide a source of organic detritus which, in total amount and season of production, provides a reasonable explanation for the major part of the input of organic matter to the deep station.

Results at the shallow station are more variable. On this side of the bay there are extensive eelgrass beds in more sheltered sites, as well as kelp beds in more exposed places. The general level of input of organic matter to the traps is consistent with substantial inputs from both these sources. The rain of phytoplankton and fecal pellets can not, of course, be ignored. However, at both stations it has been shown that the major peaks in sedimentation are not at times of peak plankton production.

POSSIBILITIES OF RESUSPENSION

About 80% of the material in the traps was inorganic, and amounted to about 1350 g m^{-2} yr^{-1} at each site. The following facts suggest that much of this material was resuspended bottom sediment. At the deep station the catch at 65 m was consistently greater than at 60 m; the percentage of organic matter in the catch was relatively constant; neither of these could be related to events in the plankton or to river runoff.

On the other hand, the organic matter content of the material in the traps was consistently higher than the organic matter content of the surface sediments. It was close to 20% in the deep station traps, while nearby bottom sediments averaged only 6.56% organic matter. It was 10.77% in the shallow-water traps, while nearby sediments had only 4.52%. The conclusion is inescapable — the organic matter in the traps was not derived primarily from resuspended benthic sediment.

Given that the organic matter was not derived from the bottom sediments, but the inorganic material may have been, the following hypothesis emerges. Marine macrophytes (kelps and seagrasses) give rise to large quantities of organic detritus, much of which, during calm weather, settles to the bottom near the place of origin. In times of storm, this material is resuspended, along with quantities of ordinary bottom sediment. The material in suspension now consists of resuspended bottom material, enriched with macrophyte and plankton detritus and it is this mixture that was caught in the sediment traps.

Discussion and Conclusions

In Cape Cod Bay, Massachusetts, Young and Rhoads (1971) found that reworking of bottom sediments by invertebrates led to the formation of an unstable surface layer which was frequently resuspended by tidal currents. Traps 80 cm above the bottom at a station 34 m deep indicated a resuspension and resettling rate of 100 g m^{-2} day^{-1}, while traps 20 cm above the bottom gave values almost 10 times greater. Turbidity measurements showed that in summer, below the thermocline, clay–silt particles were held in suspension at concentrations greater than 5 mg/liter, and that the concentration increased down to 42 m, the maximum depth studied.

Even higher rates of resuspension and sedimentation were observed in the strongly tidal estuary of the Lower York River, Virginia (Patten et al. 1966). However, it was shown that inorganic particles sank 5–6 times faster than organic particles.

The situation in St. Margaret's Bay is quite different. Observations from a submersible down to 70 m and from frequent SCUBA dives to 20 m indicate that visibility is normally good, turbidity low. The tidal flow is small compared with the volume of water in the bay, so that tidal currents are generally weak. The sediment distribution map (Hughes et al. 1972) indicates that while fine, soft sediments are present near the deepwater station, the area round the shallow station consists of poorly sorted gravels, interspersed with pockets of finer material.

The fact that the trap at 65 m consistently took more sediment, with a lower organic content, than the trap at 60 m suggests a gradient of resuspended material in the water column. However, the bottom sediments had, at most, one third the content of organic matter compared with material in the traps. Hence, even if all the inorganic matter in the traps originated by resuspension, not more than one third of the organic matter could have come from this source.

At the shallow station there was no indication of a gradient of material between 96 and 197 cm from the bottom (Table 1). There was also a consistently higher content of organic matter in the traps than in neighboring sediments. Except for the isolated occurrences of large catches which may have been caused by storm-induced resuspension, it seems reasonable to assume that here, too, most of the organic matter originated outside the area of study.

The integrated figure for organic settlement: 118 g C m^{-2} yr^{-1} at the deep station and 134 g C m^{-2} yr^{-1} at the shallow station together suggest that benthic habitats in the bay are receiving at least 100 g C m^{-2} yr^{-1}, derived from primary production and that the greater part probably originates in the dense beds of macrophytes in shallow water.

Hargrave (1973) estimated that sediments in the bay consumed 298 liters of oxygen m^{-2} per year. Assuming a respiratory quotient of 0.85, this would be enough oxygen to metabolize about 125 g C m^{-2} yr^{-1}, which is in fair agreement with the figures given above.

The question then arises, how much of this carbon flow is channeled through macroinvertebrates which form the food of fish? At present, no clear answer is possible. In various marine situations it has been estimated that bacteria account for 31–64% of benthic community respiration (Smith et al. 1972, 1973). Dale (1974) working in a Nova Scotia inlet found that the biomass of aerobic and anaerobic bacteria in intertidal sediments was about equal to the biomass of macroinvertebrates. This is consistent with the results quoted above on the partitioning of community respiration.

We may conclude that benthic organisms other than bacteria in St. Margaret's Bay receive a supply of organic matter which is of the order of 60–70 g C m^{-2} yr^{-1}, or 600–700 kcal m^{-2} yr^{-1}.

Acknowledgments

We thank M. Hodgson, N. Prouse, P. Wainwright and other colleagues in the Bedford Institute of Oceanography for assistance in the field and in the laboratory. Mr W. B. Bancroft of Nova Scotia Power Corporation kindly supplied values of rainfall and river runoff. Drs L. M. Dickie, R. J. Conover, and B. Hargrave criticized drafts of the manuscript. K. H. Mann was in receipt of an operating grant from the National Research Council.

Burke, M. V., and K. H. Mann. 1974. Productivity and production:biomass ratios of bivalve and gastropod populations in an Eastern Canadian estuary. J. Fish. Res. Board Can. 31: 167–177.

Dale, N. G. 1974. Bacteria in intertidal sediments: factors related to their distribution. Limnol. Oceanogr. 19: 509–518.

Hargrave, B. T. 1973. Coupling carbon flow through some pelagic and benthic communities. J. Fish. Res. Board Can. 30: 1317–1326.

Harrison, P. A., and K. H. Mann. 1975. Chemical changes during the seasonal cycle of growth and decay in eelgrass (*Zostera marina* L.) on the Atlantic coast of Canada. J. Fish. Res. Board Can. (In press)

Holm-Hansen, O., C. J. Lorenzen, R. W. Holmes, and J. D. H. Strickland. 1965. Fluorometric determination of chlorophyll. J. Cons. Cons. Int. Explor. Mer 30: 3–15.

Hughes, R. N., D. L. Peer, and K. H. Mann. 1972. Use of multivariate analysis to identify functional components of the benthos in St. Margaret's Bay, Nova Scotia. Limnol. Oceanogr. 17: 111–121.

Lorenzen, C. J. 1965. A note on the chlorophyll and phaeophytin content of the chlorophyll maximum. Limnol. Oceanogr. 10: 482–483.

Mann, K. H. 1972a. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Mar. Biol. 14: 199–209.

1972b. Macrophyte production and detritus food chains in coastal waters. Mem. Ist. Ital. Idrobiol. (Suppl. 29) p. 353–383.

Paranjape, M. A., and R. J. Conover. 1973. Zooplankton of St. Margaret's Bay, 1968 to 1971. Fish. Res. Board Can. Tech. Rep. 401: 83 p.

Patten, B. C., D. K. Young, and M. H. Roberts Jr. 1966. Vertical distribution and sinking characteristics of seston in the Lower York River, Virginia. Chesapeake Sci. 7: 20–29.

Peer, D. L. 1970. Relation between biomass, productivity, and loss to predators in a population of a marine benthic polychaete, *Pectinaria hyperborea*. J. Fish. Res. Board Can. 27: 2143–2153.

Platt, T. 1971. The annual production by phytoplankton in St. Margaret's Bay, Nova Scotia. J. Cons. Cons. Int. Explor. Mer. 33: 324–334.

PLATT, T., AND B. IRWIN. 1970. Primary productivity measurements in St. Margaret's Bay, 1968–1970. Fish. Res. Board Can. Tech. Rep. 203: 68 p.

RICHARDS, S. W., AND G. A. RILEY. 1967. The benthic epifauna of Long Island Sound. Bull. Bingham Oceanogr. Collect. 19: 89–135.

RILEY, G. A. 1956. Oceanography of Long Island Sound, 1952–54. IX. Production and utilization of organic matter. Bull. Bingham Oceanogr. Collect. 15: 324–344.

1970. Particulate organic matter in sea water. Adv. Mar. Biol. 8: 1–118.

SANDERS, H. L. 1956. Oceanography of Long Island Sound, 1952–54. X. The biology of marine bottom communities. Bull. Bingham Oceanogr. Collect. 15: 345–414.

SMITH, K. L. JR., K. A. BURNS, AND J. M. TEAL. 1972. *In situ* respiration of benthic communities in Castle Harbor, Bermuda. Mar. Biol. 12: 196–199.

SMITH, K. L. JR., G. T. ROWE, AND J. A. NICHOLS. 1973. Benthic community respiration near the Woods Hole sewage outfall. Estuarine Coastal Mar. Sci. 1: 65–70.

STEELE, J. H., AND I. E. BAIRD. 1972. Sedimentation of organic matter in a Scottish Sea Loch. Mem. Ist. Ital. Idrobiol. (Suppl. 20) p. 73–88.

STEPHENS, K., R. W. SHELDON, AND T. R. PARSONS. 1967. Seasonal variations in the availability of food for benthos in a coastal environment. Ecology 48: 852–855.

SUTCLIFFE, W. H. JR. 1972. Some relations of land drainage, nutrients, particulate material, and fish catch in two eastern Canadian Bays. J. Fish. Res. Board Can. 29: 357–362.

WALKLEY, A. 1947. A critical examination of a rapid method for determining organic carbon in soils — Effect of variations in digestion conditions and of inorganic soil constituents. Soil Sci. 63: 251–264.

YENTSCH, C. S., AND D. W. MENZEL. 1963. A method for determination of phytoplankton chlorophyll and phaeophytin by fluorescence. Deep-Sea Res. 10: 221–231.

YOUNG, D. K. AND D. C. RHOADS. 1971. Animal-sediment relations in Cape Cod Bay, Massachusetts. I. A Transect study. Mar. Biol. 11: 242–254.

ZEITZSCHEL, B. 1965. Sur Sedimentation von Seston, eine productions-biologische Untersuchung von Sinkstoffen und Sedimentation der Westlichen und mittleren Ostsee. Kieler Meeresforsch. 21: 55–80.

Summer Distribution of the Nearshore Fish Community near a Thermal Generating Station as Determined by Acoustic Census

JOHN R. M. KELSO AND C. K. MINNS

Department of the Environment, Fisheries and Marine Service, Great Lakes Biolimnology Laboratory, Canada Centre for Inland Waters, Burlington, Ont. L7R 4A6

KELSO, J. R. M., AND C. K. MINNS. 1975. Summer distribution of the nearshore fish community near a thermal generating station as determined by acoustic census. J. Fish. Res. Board Can. 32: 1409–1418.

The relation between thermal plumes and fish abundance and distribution was studied at the Pickering Nuclear Generating Station, Lake Ontario, using simultaneous digital echo counting and temperature monitoring systems during summer thermal stratification of the lake.

Fish relative abundance varied from 20.8/10,000 m^3 to 1,037/10,000 m^3 and both these extreme density estimates occurred in the 7.5–12.5-m depth shell. Also, changes in distribution of the nearshore community were apparent during the study period, July–October. The fish community in July was pelagic and selected 10–11 C and 14–16 C. That same community later appeared to become segregated into benthic and pelagic communities. Thermal plumes, either well defined or diffuse, appeared to have little effect on the pelagic community either because fish were not available to elevated temperatures by habitat selection or because fish failed to respond to increased surface temperatures.

KELSO, J. R. M., AND C. K. MINNS. 1975. Summer distribution of the nearshore fish community near a thermal generating station as determined by acoustic census. J. Fish. Res. Board Can. 32: 1409–1418.

Nous avons étudié la relation entre les zones superficielles thermiques et l'abondance et la distribution des poissons à la centrale nucléaire de Pickering, lac Ontario, en utilisant des systèmes simultanés de comptage numérique acoustique et de contrôle continu des températures durant la période de stratification thermique d'été du lac.

L'abondance relative du poisson varie de 20.8/10,000 m^3 à 1,037/10,000 m^3, et ces deux extrêmes d'estimé de densité se rencontrent tous deux dans l'intervalle de profondeur de 7.5 à 12.5 m. De plus, des changements dans la répartition des communautés du littoral sont apparentes durant la période d'étude, de juillet à octobre. La communauté de poissons en juillet est pélagique et choisit des températures de 10–11 C et 14–16 C. Plus tard, cette communauté semble se séparer en communautés benthiques et pélagiques. Les zones superficielles thermiques, qu'elles soient bien définies ou diffuses, semblent avoit peu d'effet sur la communauté pélagique, soit parce que les poissons, par un choix d'habitat, évitent les températures élevées, soit parce que les poissons manquent de réagir aux températures élevées de la surface.

Received July 25, 1974
Accepted April 7, 1975

Reçu le 25 juillet 1974
Accepté le 7 avril 1975

THE advent of echo processing techniques (Dowd 1967; Thorne 1971; Kelso et al. 1974; and others) is enabling fisheries scientists to rapidly discern features of fish abundance and distribution previously determined only by time-consuming techniques. Simultaneous application of acoustic and water-quality monitoring procedures (Spigarelli et al. 1973) allows fish distribution to be related to environmental factors. Many variables are recognized as influencing fish distribution. This study contributes to the examination of the complex relations between a nearshore fish community and its habitat.

In the nearshore habitat, thermal discharges are known to alter species composition in discharge canals (Coutant 1970) and movement patterns, particularly of fish encountering the turbulent mixing zone (Kelso 1974). Evaluations of thermal addition, however, necessitate an examination of the response of fish in large areas under the general influence of a plume in addition to effects resulting from entrainment and those locally existing in discharge canals. Only by synthesis of these aspects of water use for cooling purposes can a firm basis for decision making relating application of water quality criteria and power plant design be reached. This study furthers the examination of the response of a nearshore fish community to thermal plumes and seeks to add to the study of fish in relation to their habitat.

Printed in Canada (J3504)
Imprimé au Canada (J3504)

TABLE 1. Plant output in megawatts (Mwe) and temperatures at intake and outfall on days of experimentation at the Pickering Nuclear Generating Station.

Date	Average plant output (Mwe)	Intake temp C(F)	Outfall temp C(F)	ΔT
July 17	no record	no record	17.7 (63.9)	
18	534	11.9 (53.4)	18.8 (65.8)	6.9
30	1081	11.9 (53.4)	17.1 (62.8)	5.2
Aug. 15	1872	17.1 (62.7)	27.2 (82.9)	10.1
16	2052	19.7 (65.9)	30.0 (86.0)	10.3
17	2096	19.9 (67.9)	31.7 (89.0)	11.8
Sept. 26	2070	16.4 (61.6)	28.2 (82.7)	11.8
28	1534	16.3 (61.3)	26.4 (79.5)	10.1
29	1535	16.4 (61.6)	26.0 (78.8)	9.6
Oct. 4	2027	17.3 (63.2)	28.2 (82.7)	10.9
			Mean	9.6

Materials and Methods

THERMAL PLUME ASSESSMENT

The Pickering Nuclear Generating Station is located on the north shore of Lake Ontario approximately 40 km east of Toronto, Ontario. During the study period, power production varied between 534 and 2096 Mwe with a mean of 1645 Mwe (Table 1). Increase in temperature during condenser cooling resulted in increases above Lake Ontario ambient from 5.2 to 11.8 C, average 9.6 C.

A series of readily visible shore markers were installed east and west of the Pickering Nuclear Generating Station (see Kelso 1974 for general description of the area and reference station position) to aid in position fixing. Reference to shore markers with sextants and radar bearings from prominent landmarks were used for positioning near the generating station. A limited area immediately south of the power plant was inaccessible as water depth was minimal.

Cruise lines were run parallel to shore and generally conformed to depth contours. Transects were between 0.2 and 2.9 km from shore and were separated by approximately 0.2 km through the first 1 km offshore and 0.4 km thereafter. Start and end positions of each transects were determined using appropriate shore references. All transects were timed by stop watch.

The towed thermistor array consisted of a Beldon six conductor neoprene jacketed electrical cable equipped with five water-tight Marsh and Marine break-outs. A Braincon 0.61-m V-fin was used as a depressor mechanism to ensure maximum vertical coverage by the towed array. Five 4 K Fenwall isocurve thermistors were lubricated with waterproof grease and placed in break-outs strategically situated to sample 0–10 m of the water column. The time constant of the thermistors was 5 s. All thermistors were calibrated according to accepted procedures. A thermistor bridge was constructed to provide a 0–500 mV output over the performance range of the thermistors and all data was stored by a five-channel strip chart recorder that provided continuous data acquisition. All data were manually extracted from the charts. Surface isotherms and vertical profiles (to the nearest degree) were subsequently constructed.

Temperature data were extracted from analog charts at 100-m intervals. If appreciable changes in temperature occurred within the 100-m interval, the appropriate data were extracted for inclusion in isotherm plots.

Depths monitored by the towed array were manually controlled by selecting the amount of cable, subsequently the number of thermistors, running free through an A-frame on the stern of the launch. Total coverage of the water column was at times impossible as rock outcrops necessitated raising the towed array. Although the thermistors were at times in the vessel's wake, innumerable independent temperature determinations indicated that recorded temperature was within ±0.2 C of the surface water temperature.

Meteorological conditions and variations in power production influenced shape and spatial distribution of the plume. Consequently search patterns were designed to correspond with the probable sector occupied and terminated when accessible areas had been examined as thoroughly as possible.

ACOUSTIC ASSESSMENT OF PELAGIC FISH

The digital echo counting system used herein has been described in detail elsewhere (Kelso et al. 1974). Briefly, the system consists of a 200 kHz echo sounder coupled by preamplifier–rectifier to a logic circuit. The logic gated echoes by four delayed pulses of 6.6 ms duration to correspond to a 5-m depth shell. Output from the logic was stored in event counters corresponding to the four 5-m depth shells between 2.5 and 22.5 m. Since the signal sorting system was unable to differentiate echoes from fish from bottom echoes, the depth shell in which the bottom echo occurred was ignored. An indication of species composition of the observed densities was provided by hoopnet catches made at two nearshore locations (Kelso 1974).

Information presented herein was selected from 19 days when the nearshore thermal regime was completely defined and operating conditions were optimal. Diel variability in plume behavior and fish community response should be expected; however, all data presented resulted from daytime observations only.

Data Analysis

Relative density (D) was calculated (Kelso et al. 1974) from echo counts over 1-min intervals (corresponds to $\simeq$ 100 m traveled) and it was converted to D/10,000 m^3 for ease in data handling and presentation. Estimates of relative density from the echo counting system were used only in descriptions of general trends of distribution and abundance (Fig. 1 and Table 2), whereas counts from the accompanying echograms were used in referencing fish to their habitat.

Echogram analysis corresponds directly to echo counts and estimates of density by trawls (see Kelso et al. 1974). Targets were subjectively classed as individuals or schools and assigned to their appropriate depths. Individual target (fish) data from July 30, September 28, September 29, October 4 were examined in detail. Schools were observed infrequently and were too few for detailed analysis. For each date, individual target data were inserted in a 3-dimensional matrix where the three axes were 1) fish depth in 1-m intervals with 0–1 m being ignored; 2) water depth in 1-m intervals, and 3) temperature in 1 C intervals. Counts were corrected for the volume sampled in each 1-m depth shell to yield relative targets/m^3. All habitat combinations of fish depth, water depth, and temperature were not equally available in the transects for any date. Therefore, transects were divided into habitat blocks, 150 m horizontally and 1 m vertically. Habitat blocks were then enumerated into a matrix with the same axes used for targets. Target matrix position counts were divided by habitat matrix counts to yield a matrix of weighted relative abundance. Position values were then expressed as a percentage of the total. Two 2-dimensional summation matrices were generated for each relative abundance matrix. Necessarily each sampling date was treated separately. The matrix analysis is conceptually different from relative (or absolute) density estimation and thus can be related to relative abundance only indirectly.

Results

THERMAL PLUMES

Temperature data was limited within 0.35 km of shore; also, temperature records were not always available near the bottom because of rock outcrops that endangered the V-fin. Nevertheless, when plumes were directed offshore at least 80% of the area under the influence of the thermal plume was studied routinely.

The thermal plume was extremely variable in nature (Fig. 1). In general during the period of study, it extended in southerly or westerly directions under the extant meteorological conditions and did not usually extend beyond 2.0 km from the discharge. No configuration could be considered "typical" for thermal regimes studied during 1973.

During times of negligible wind (August 15, September 28, October 4), the shape of the thermal plume was somewhat more conventional as the axis extended directly off the discharge and maintained its feather-like shape. Onshore winds (July 17, 18; August 16; September 26, 29) tended to elongate the plume parallel to shore. During an offshore wind, the plume retained its integrity (August 17), but the central axis was displaced according to wind direction. On July 30 during an onshore wind, a surface plume was not detected and nearshore temperatures were noticeably lower than offshore Lake Ontario temperatures. On several occasions (Fig. 1), Frenchman's Bay and its connecting channel exerted a minor warming role on the nearshore thermal structure.

FISH DENSITY AND DISTRIBUTION

Fish density and distribution varied appreciably during the investigation (Table 2). During July when temperature in the uppermost depth shell was lowest, fish were consistently more abundant in that strata (2.5–7.5 m). Relative abundance was lowest in the 2.5–7.5 m strata when temperatures were highest (August 17). Generally, when temperatures tended toward homogeneity, (August 17, September 26, September 29, October 4) fish were more evenly distributed vertically and abundance tended to become similar in the two depth shells (Table 2). However, an exception occurred August 16 as temperature was reasonably homogeneous but density was greater in the 7.5–12.5 m depth shell. From echograms, it was determined that on August 16, when greatest abundance was detected, most fish were in schools. Echograms indicated that schools (alewives and smelt) contributed frequently to

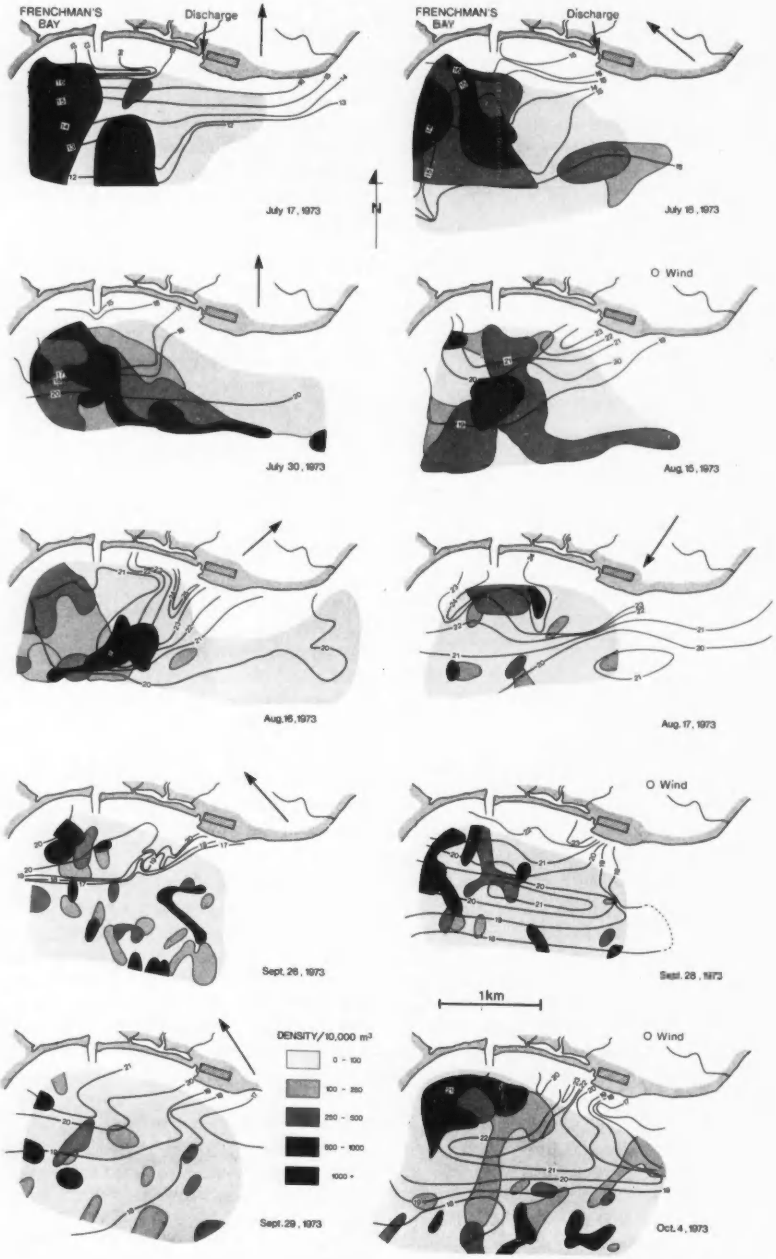

FRENCHMAN'S BAY
Discharge
July 17, 1973
FRENCHMAN'S BAY
Discharge
July 18, 1973
N
July 30, 1973
O Wind
Aug. 15, 1973
Aug. 16, 1973
Aug. 17, 1973
Sept. 28, 1973
O Wind
Sept. 28, 1973
1km
DENSITY/10,000 m³
0 - 100
100 - 250
250 - 500
500 - 1000
1000 +
Sept. 29, 1973
O Wind
Oct. 4, 1973

FIG. 1. Density and horizontal distribution of the Lake Ontario nearshore fishery in relation to the thermal plume.

TABLE 2. Average estimate of abundance (D/10,000 m^3) obtained from two depth shells and range in temperature (C) for those depth shells for each census date.

Census date 1973	D/10,000 m^3 2.7–7.5 m	Range in temp (C)	D/10,000 m^3 7.5–12.5 m	Range in temp (C)
July 17	608.9	11.3–8.1	33.1	8.3–<6
July 18	503.2	13.7–8.8	32.7	11.4–8.3
July 30	898.3	18.1–>6	20.8	7.3–<5
Aug. 15	381.0	20.1–13.4	413.3	14.7–<10
Aug. 16	269.8	20.7–17.0	1037.3	19.0–16.2
Aug. 17	107.7	21.5–18.5	72.4	19.8–≈17
Sept. 26	198.1	18.4–15.3	139.0	16.1–<15
Sept. 28	523.3	19.8–16.5	184.4	16.8–≈12
Sept. 29	332.6	19.1–16.4	141.9	<17
Oct. 4	202.6	20.3–16.6	122.3	<17

abundance estimates particularly in the offshore area.

Distribution of the nearshore fish community (Fig. 1) was extremely variable in the study area and constancy between analyses existed in only several broad areas. On days when the plume possessed a well-defined shape (August 15; September 26, 28; October 4) the region subject to greatest increase in temperature above ambient had the lowest density of fish (Fig. 1). However, on all days of analysis this area (directly related to the discharge and generating station) always exhibited the lowest density. Also, the area directly south of the generating station was sparsely populated (Fig. 1). Fish were usually more abundant in the western portion of the study area where depth sharply increased. Although it is not apparent from Fig. 1, fish were generally more abundant when depth was either sharply increasing or sharply decreasing. Scattered areas of high density existed offshore and appeared to be large aggregations of alewives (see Kelso et al. 1974 for description of traces).

Hoopnet catches (Kelso 1974) indicated that the community within 1 km of shore was dominated by brown bullhead (90%) followed by carp, white sucker, yellow perch, and white perch. The pelagic community existed offshore, determined from echogram inspection (Kelso et al. 1974) was largely composed of alewives (80%), smelt (15%), yellow perch, and white perch.

In the relative abundance matrices for all 4 days examined (Table 3), clumping by habitat within the nearshore fish community can be recognized. Undoubtedly, this reflects the presence of benthic and pelagic fish species. The two fish groupings can be observed primarily in the relative depth frequencies, though in the July 30 matrix, the separation is noticeable only in the temperature distribution with peaks occurring in the 10–11 C and 14–16 C ranges (Table 3). Separation of the groups by temperature is also noticeable in the September 29 and October 4 matrices. Thus, there are at least two subcommunities in the nearshore community and they could be characterized as benthic (both warm and cold) and pelagic. In early summer (Table 3, July 30), temperature stratification is poorly developed and there is an apparent intermixing of the subcommunities. Later (September and early October) stratification is stronger and spatial separation is almost complete.

Comparison of the relative abundance matrices for September 28 and 29 (Table 3), which can be characterized as "plume" and "non-plume" days, respectively (Fig. 1), reveals little or no difference, particularly in the near-surface layers. Thus the presence of a well-developed thermal plume does not appear to be affecting the distribution of the nearshore fish community. In the July 30 matrix (Table 3), the fish were found predominately in the 5–8 m depth range, below the normal depth penetration of any thermal plume. The matrix, for October 4 when a well-developed plume was present (Fig. 1), is similar to those of the September matrices (Table 3).

Discussion

Both fish density and distribution and thermal plumes are liable to extremely rapid changes and the technique used herein provided the only feasible means of rapidly examining the relation between the nearshore fish community and thermal structure. The technique, however, has limitations. Modifications advantageous to the per-

TABLE 3. Percentage matrices of relative fish abundance in relation to habitat characteristics, weighed for habitat abundance.

	July 30																												
	Water depth (*m*)													Temperature (*C*)															
	5	6	7	8	9	10	11	12	13	14	15	16	Total	<6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1–																													
2–																													
3–		2.0			0.6								2.6							2.0		0.6							
4–		2.4			0.3	1.5	0.2	0.7	0.1		0.8		6.0							2.4	2.0			0.5		1.1			
5–		0.5			1.7	0.9	1.1	4.8	0.8		2.2	3.5	15.5		0.4	0.6	0.6	2.1			1.1	0.9	3.0	4.3	2.5				
6–		0.5			0.1	1.2	3.6	16.3	0.4	3.8	6.1	0.8	32.8	0.1	1.1				6.7	1.9	5.9	5.9	4.9	6.3					
7–					0.6	1.2	1.7	11.4	3.0	2.5	4.3	0.8	25.5	0.3				0.6	5.9	4.0		5.5	5.3	3.9					
8–					1.2	1.4	0.6	3.8	2.2	0.7	0.4	0.3	10.6	1.9	1.0				1.5	1.0		1.4	3.8						
9–					0.3	1.5	0.1	0.8	0.8	0.4	0.2		4.2	2.3	1.0				0.8										
10–								0.4	0.5	0.2			1.1	1.1															
11–							0.1	0.4	0.4	0.1			1.0	1.0															
12–								0.2	0.2	0.1			0.5	0.5															
13–									0.1	0.2			0.3	0.3															
14–																													
15–																													
16–																													
Total		5.4			4.8	7.7	6.4	38.8	8.5	8.0	14.0	5.4	100.0	6.5	3.5	0.6	0.6	2.7	14.9	11.3	9.0	14.3	17.0	15.0	2.5	1.1			

TABLE 3. (*Continued*)

	September 28																				
	Water depth (*m*)														Temperature (*C*)						
	3	4	5	6	7	8	9	10	11	12	13	14	15	Total	<17	18	19	20	21	22	23
1–								2.3	2.2	1.1				5.6			1.1	0.5	4.0		
2–		4.5				4.1	11.8	1.8	2.6	5.3	2.5			32.6		14.5	15.6	2.5			
3–		2.0	2.1			0.7	1.2							6.0		5.9					
4–			5.2	0.7			0.4	0.3	0.1	0.4				7.1	0.8	5.9	0.4				
5–				16.0		0.3	1.2	0.3						17.8	5.3	12.6					
6–					1.7	1.3	0.8	0.1						3.9	1.5	2.5					
7–						1.8	3.0	0.4					0.3	5.5	3.4	2.3					
8–							3.9	2.0	0.5			0.1	0.3	6.8	5.3	1.5					
9–								4.0	1.1	0.1	0.2	0.2	0.3	5.9	5.9						
10–									0.6	0.2	0.8	0.3	0.3	2.2	2.3						
11–											1.3	0.8	0.9	3.0	3.0						
12–												1.5	1.1	2.6	2.6						
13–													0.8	0.8	0.8						
14–																					
15–																					
Total		6.5	7.3	16.7	1.7	8.2	22.3	11.2	7.1	7.1	4.8	2.9	4.0	100.0	30.9	45.2	17.1	3.0	4.0		

TABLE 3. (*Continued*)

	September 29																							
	Water depth (*m*)																	Temperature (*C*)						
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total	<17	18	19	20	21	22	23
1–																								
2–			25.7														25.7					25.7		
3–			5.4			16.4		5.9									27.7	1.8	0.3	20.2		5.4		
4–		2.9	1.9	0.8	0.8	0.3	1.5	1.1	0.2			0.3				2.4	12.2	4.6	5.3	2.3				
5–			9.1			0.2						0.6	0.3				10.2	9.4	0.8					
6–				0.5			0.1						0.2				0.8	0.6	0.2					
7–						0.1					0.1			0.5		0.5	1.2	1.2						
8–						0.1	0.1		0.1		0.1		0.2				0.6	0.6						
9–							0.8	0.6	0.2		0.2	0.2	0.4				2.4	2.4						
10–								0.4	0.7	0.2	0.4	0.3					2.0	2.0						
11–									0.2	0.8	1.6	0.7					3.3	3.3						
12–										0.4	1.6	1.9	0.4				4.3	4.3						
13–											0.6	1.3	0.8				2.7	2.7						
14–												0.5	0.7	0.1			1.3	1.3						
15–													1.0	0.5	0.4		1.9	1.9						
16–														1.8	1.2	0.6	3.6	3.6						
17–															0.4	0.2	0.6	0.6						
18–																0.1	0.1	0.1						
Total		2.9	42.1	1.3	0.8	17.1	2.5	8.0	1.4	1.4	4.6	5.8	4.0	2.9	2.0	3.8	100.0	40.4	6.6	22.5		31.1		

TABLE 3. (*Concluded*)

October 4	Water depth (*m*)																	Temperature (*C*)						
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Total	<17	18	19	20	21	22	23
1–				18.3	5.5	2.0		0.7			1.8						28.3		1.8	0.7	16.6	2.0	7.2	
2–		6.0	3.6	4.3	4.5	6.9	6.6	3.3		3.4	0.5	0.5	1.0				40.6		5.6	9.5	9.0	16.4		
3–		1.1	0.2	0.1	0.4	2.6		1.1		2.3	0.4	0.7	0.1		0.5		9.5	0.6	3.2	3.5		2.2		
4–			0.2		0.1	0.3	0.1	0.1		0.1	0.1	0.1	0.1				1.2	0.7	0.5					
5–			2.1	0.2	0.3		0.2		0.1		0.1		0.1				3.1	2.9	0.2					
6–				0.3	0.3								0.2				0.8	0.7	0.1					
7–					0.6	0.3	0.2	1.2	0.1			0.1	0.1	0.1			2.7	1.6	1.2					
8–						0.1	0.5	0.1	0.1		0.1	0.1	0.2				1.2	1.2						
9–							0.1	0.4	0.1	0.1	0.1	0.2	0.2	0.2			1.7	1.7						
10–								0.4	0.5	0.5	0.4	0.2	0.1	0.1	0.1		2.3	2.3						
11–									0.4	0.5	0.8	0.3	0.2	0.2	0.3		2.5	2.5						
12–										0.2	0.7	0.5	0.4	0.3	0.2		2.3	2.3						
13–											0.4	0.4	0.5	0.6	0.5		2.4	2.4						
14–												0.3	0.5	0.6	0.4		1.8	1.8						
15–													0.1	0.1	0.3		0.5	0.5						
16–															0.2		0.2	0.2						
17–																								
18–																								
Total		7.1	6.1	23.2	11.7	12.2	7.7	7.3	1.6	7.1	5.5	3.3	3.8	2.2	2.5		100.0	21.6	12.5	13.7	25.6	20.6	7.2	

formance of the digital echo counting system have been described elsewhere (Kelso et al. 1974). The disadvantages of the system that affect this study are the loss of digital acoustic data in the top 2.5 m (partially overcome by the use of echogram analysis) and the loss of information from the depth shell in which the bottom echo occurs. Also, although schools were infrequent at Pickering, digital echo counting systems tend to underestimate high densities. A greater limitation of the Pickering studies was imposed not by techniques or technology but by local lake morphometry which limited the accessible area and by rapidly changing weather which at times rapidly altered the nearshore thermal structure and in all likelihood the associated fish community.

Seasonal changes in the nearshore community were apparent (Table 2, Table 3) although from sparse data (Kelso 1974) species was similar. The two groupings of fish (benthic and pelagic) appearing on the basis of temperature selection in the July 30 sampling, peak abundance occurring at 10–11 and 14–16 C, subsequently selected habitats that were either benthic — both nearshore and offshore — or pelagic (Table 3). When the range in available habitat temperatures became less (Table 2), acoustic estimates in the two depth shells indicated a decreased preference for pelagic environments (probably those that selected 10–11 C early in the study). Published information for temperature preference is available for only a limited number of species encountered at Pickering (brown bullhead, white sucker, and yellow perch) and combined with our only partial knowledge of species composition for abundance estimates leaves us unable to discuss the seven major species of the Pickering nearshore fish community. The pelagic community is undoubtedly alewives and smelt and these species apparently seek habitats of higher temperatures (Table 3). Part of the benthic community, likely bullhead, carp, and white sucker (Kelso 1974), appeared to remain nearshore during most of the study period (Fig. 1 and Table 3).

Thermal plumes did not appear to greatly influence abundance or distribution of the Lake Ontario nearshore fish community to an appreciable extent during the study period. When surface plumes extended offshore, the pelagic subcommunity (that most likely to be affected by plumes) either selected habitats well below the surface, July 30, or if in the surface layers did not appear to alter its pattern of distribution (Table 3). Spigarelli et al. (1973) detected general localizations by temperature and depth but little detectable response in relation to thermal plumes. Neill and Magnuson (1974) detected influences of thermal addition to Lake Monona fisheries but lacked resolution as to where in the thermally altered region the response occurred and was unable to capsulize the adjustments, or lack of them, performed by the community studied.

Although thermal plumes appeared to have little difference on the Lake Ontario nearshore community, discharge canals and turbulent mixing zones may produce altered responses in terms of movement (Kelso 1974) or habitat selection. Furthermore, seasonal and diel changes may place nearshore communities in more vulnerable locations. Although our knowledge of habitat selection and effects of thermal addition are increasing, our understanding of both local and broad effects remains elementary.

Acknowledgments

W. H. Hyatt proved invaluable during the experiments conducted at the Pickering Generating Station. Vessel support and the assistance of M. G. Head on the launch, from the Canada Centre for Inland Waters, enabled the assessments of fish and temperature. Ontario Hydro was most cooperative. M. G. Johnson's encouragement and friendly criticism were most welcome.

COUTANT, C. C. 1970. Biological aspects of thermal pollution. 1. Entrainment and discharge canal effects. Crit. Rev. Environ. Control 1: 341–381.

DOWD, R. G. 1967. An echo counting system for demersal fishes. FAO conference on fish behaviour in relation to fishing techniques and tactics. FAO Fish. Rep. 2: 315–321.

KELSO, J. R. M. 1974. Movement of brown bullhead (*Ictalurus nebulosus*) near a thermal generating station as determined by ultrasonic tracking. J. Fish. Res. Board Can. 31: 1507–1513.

KELSO, J. R. M., R. G. DOWD, AND E. E. PICKETT. 1974. A digital echo counting system for determining abundance of pelagic fish in relation to depth. J. Fish Res. Board Can. 31: 1101–1104.

NEILL, W. H., AND J. J. MAGNUSON. 1974. Distributional ecology and behavioral thermoregulation of fishes in relation to heated effluent from a power plant at Lake Monona, Wisconsin. Trans. Am. Fish. Soc. 103: 663–710.

SPIGARELLI, S. A., G. P. ROMBERG, AND R. E. THORNE. 1973. A technique for simultaneous echo location of fish and thermal plume mapping. Trans. Am. Fish. Soc. 102: 462–466.

THORNE, R. E. 1971. Investigations into the relation between integrated echo voltage and fish density. J. Fish. Res. Board Can. 38: 1269–1273.

Size Selective Predation by Juvenile Chum Salmon (*Oncorhynchus keta*) on Epibenthic Prey in Puget Sound[1]

ROBERT J. FELLER AND VICTOR W. KACZYNSKI[2]

Department of Oceanography, University of Washington, Seattle, Wash. 98195, USA

FELLER, R. J., AND V. W. KACZYNSKI. 1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. J. Fish. Res. Board Can. 32: 1419–1429.

Analysis of gut contents shows that juvenile (30–50 mm) chum salmon (*Oncorhynchus keta*) in Puget Sound select epibenthic organisms as their primary prey. Harpacticoid copepods numerically comprised over 80% of their natural diet in two areas studied, while terrestrial insects and cladocerans were most important in a third area. Calculation of Ivlev (1961) electivity coefficients indicated high selectivity factors for harpacticoids at one site (+0.59 to +0.94). Comparison of fish gut contents with quantitative epibenthic pump samples of available prey shows that prey selection was size related, but opposite that currently reported in the literature (e.g. Brooks and Dodson 1965); that is, the smaller of the available prey was preferred. This was true for both the total available prey size spectrum and the harpacticoid copepod fraction of the prey spectrum. Large numbers of prey eaten per fish suggest that juvenile chum salmon may exert high predation pressure on nearshore epibenthic organisms in Puget Sound during spring.

FELLER, R. J., AND V. W. KACZYNSKI. 1975. Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound. J. Fish.Res. Board Can. 32: 1419–1429.

Des analyses du contenu de l'appareil digestif démontrent que les jeunes (30–50 mm) saumons keta, *Oncorhynchus keta*, sélectionnent les organismes épibenthiques comme proie principale dans le Puget Sound. D'un point de vue numérique, les copépodes harpacticoïdes participent pour plus de 80% du régime en deux endroits, et les insectes d'origine terrestre ainsi que les cladocères sont les plus importants au troisième endroit étudié. Les coefficients d'électivité d'Ivlev (1961) sont très élevés à l'un des sites (+0.59 à +0.94). Une comparaison du contenu de l'appareil digestif des poissons avec des échantillons quantitatifs épibenthiques prélevés par pompage montre que la sélection est fonction de la taille, mais dans un sens opposé à celui récemment décrit dans d'autres publications (e.g. Brooks et Dodson 1965); en d'autres termes, la plus petite des proies disponibles fut préférée. Ceci est valable vis-à-vis de l'éventail des tailles des proies disponibles ainsi que de l'éventail de la fraction copépode harpacticoïde des proies. Le grand nombre de proies dévorées par poisson suggère que les jeunes saumons sont capables d'appliquer une pression de prédation élevée sur leurs proies épibenthiques du littoral dans le Puget Sound au cours du printemps.

Received November 15, 1974
Accepted April 2, 1975

Reçu le 15 novembre 1974
Accepté le 2 avril 1975

THE movements of juvenile pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*) immediately after migration to marine waters are fairly well known. Manzer (1956), Gilhousen (1962), Kirkwood (1962), LeBrasseur and Parker (1964), and Kaczynski et al. (1973) have observed that these fish inhabit nearshore areas in relatively shallow water for a period of 2–3 mo and then move offshore into deeper water when they have reached a length of about 60 mm. The diet of these fish in the coastal waters of the northeast Pacific Ocean is not well known, particularly for juvenile (30–50 mm) chum salmon.

Before the publication by Kaczynski et al. (1973) concerning young pink and chum salmon in shallow nearshore waters, the available literature suggested that the natural diet of juvenile chum salmon is largely planktonic (Foskett 1951; Barraclough et al. unpublished data; Manzer 1969; Merrell 1970). These later studies were done on slightly larger and presumably older fish captured in deeper waters. The former study is

---

[1] Contribution No. 833 from the Department of Oceanography, University of Washington, Seattle, Wash. 98195, USA.

[2] Present address (V.W.K.): BEAK Consultants, Inc., 1336 SW 2nd Ave., Portland, Oreg. 97201, USA.

Printed in Canada (J3620)
Imprimé au Canada (J3620)

the only published description of the diet of juvenile pink and chum salmon from Puget Sound, and it was found that epibenthic organisms comprised the main part of their diet during their onshore period of development. Prey availability was found to affect feeding, and this could cause dietary differences between regions.

This paper further describes and substantiates the natural epibenthic diet of juvenile chum salmon from three areas of Puget Sound. In addition, the stomach contents of the fish are compared with abundance and size of prey organisms as determined from quantitative intertidal epibenthic pump samples collected concurrently with the fish during April and May 1971.

Materials and Methods

The three sampling areas were Toandos Peninsula in Dabob Bay, Hood Canal (47° 43′ N, 122° 48′ W), Port Susan in east central Puget Sound 47° 52′ N, 122° 22′ W), and Anderson Island in southern Puget Sound (47° 11′ N, 122° 41′ W). All three areas have nurtured large stocks of juvenile chum salmon in the past and were chosen for study because they represent typical onshore habitats of these fish in Puget Sound, Wash. The beaches are composed of sand, gravel, and cobbles at high tide levels and consist of coarse sand at mid- to low tide levels. Tidal range during the study was 3–4 m. All sampling was designed to be done during the midafternoon low tide; however, on several occasions time constraints did not allow all samples to be taken at the same tidal stage.

The sampling techniques used in this study were similar to those described by Kaczynski et al. (1973). Briefly, fish were collected from shore with a long-handled dipnet. Six chum were arbitrarily taken from the net and immediately fixed in 10% formalin. No regurgitation or defecation was observed during this procedure. The entire intestinal tract of each fish was excised and opened individually in the lab. Gut contents were identified, counted, and measured to the nearest 0.1 mm under a binocular dissecting microscope. Intertidal benthic pump samples were taken along a 100-m transect parallel to the beach in the area where the fish were captured, using a high-speed water pump that delivered 125 liters/min. A 0.5-m^2 raised screen hoop was placed in the water at a depth of ½ m and the 5-cm diam pump hose was passed systematically over the sediment enclosed within the hoop. A brass probe at the entrance to the hose mouth served to keep the mouth 2–3 cm above the sediment while it thoroughly agitated the sand to a depth of 2–3 cm. Water was pumped for 3 min into a 195-μm net, and the organisms, detritus, and sand collected were washed into glass jars for preservation in 10% formalin.

The pump samples were examined in the lab where organisms were completely removed by progressive decantation, identified, counted, and measured to the nearest 0.1 mm. Size of the organisms was based on total length less setae and minor appendages. Harpacticoid copepods were measured from the tip of the rostrum to the basal segment of the caudal furcae. The larger samples were split once with a Folsom plankton splitter and half the sample was analyzed.

The gut contents were well preserved and relatively easy to identify, and intact organisms were found along the entire length of the gut. Less than 5% by number of all organisms found in all fish examined could not be identified. These were not included in the size-frequency analyses or in the dietary descriptions.

For the purpose of this study, epibenthic organisms are considered to be those that live very near, on, or slightly within the sediment surface. These include gammarid amphipods, harpacticoid copepods, barnacle cyprids, cumaceans, and settled invertebrate eggs. Calanoid copepods, euphausiids, barnacle nauplii, cladocerans, larvaceans, decapod zoea, and hyperiid amphipods are considered planktonic, and all insects are considered of terrestrial origin. Certain other organisms found in the pump samples were designated as unavailable as prey for the juvenile salmon. These included polychaetes and bivalve molluscs because of their burrowing habits, and hard-shelled gastropods because of their indigestibility. Any organisms longer than the average unextended jaw length (tip of snout to posterior edge of operculum) of the six fish examined on each date were considered too large to be eaten. Such unavailable organisms were not included in the size-frequency analyses and comprised less than 0.1% by number of the total number of organisms found in all fish examined.

Size-frequency and cumulative size-frequency distributions were drawn for prey available and eaten on each date. Similar size-frequency distributions were drawn for the harpacticoid copepod fraction of prey available and eaten on each date. Both the mean size of the eaten and of the available fraction of these size-frequency distributions and the size-frequency distributions themselves were tested for significant differences using nonparametric procedures because all such distributions were non-normal when plotted on probability paper.

Electivity coefficients (Ivlev 1961) were calculated using the relation $E = r_i - p_i/r_i + p_i$, where r_i is the proportion of a particular prey type in the diet of the fish, and p_i is the proportion of that same prey type available in the environment. E takes on values from -1 to $+1$, with positive values indicating selection, zero indicating that prey were taken in direct proportion to their abundance in the environment, and negative values indicating rejection or avoidance of the prey organism.

We estimated the number of juvenile chum salmon residing in the three nearshore beach areas by visually counting fish in schools while either walking along shore or traveling in a boat moving slowly and quietly parallel to shore. On each survey date a total of 12.6 km of beach at Dabob Bay, 14.1 km at Anderson Island, and 18.2 km at Port Susan was inventoried.

Results

DIETARY DESCRIPTION

A total of 78 chum fry were captured and examined: 30 from Dabob Bay, 18 from Anderson Island, and 30 from Port Susan. All fish had food in their guts. No attempt was made to estimate volume or fullness of the gut; however, a trend toward greater numbers of prey per fish with time is evident (Table 1).

Food items at Dabob Bay and Anderson Island were very similar, with harpacticoid copepods comprising 66–97% by number of the diet. Port Susan chums fed primarily upon terrestrial and marine insects (adult Diptera and chironomid larvae), cladocerans (*Podon* and *Evadne* sp.), gammarid amphipods, and generally contained considerably fewer prey per fish and a slightly greater variety of prey.

In numerical order, the four most important items in the diet of all fish combined ($N = 78$) were harpacticoid copepods, gammarid amphipods, euphausiids, and insects. This ranking is based on frequency of occurrence and as such does not reflect the importance of the different prey items either numerically (see Table 1) or volumetrically. For instance, one large euphausiid may occupy as much space in the gut as 10 or 20 harpacticoids.

The coefficient of variation (standard deviation/mean × 100) was calculated for separate prey items from the six fish on each date at each location. At Dabob Bay and Anderson Island the coefficients were very low for the dominant prey item, the harpacticoids, ranging from 2.5 to 40.7%. The other numerically less important prey occurred in much more variable proportions in fish on any given sampling date and location; coefficients of variation for these prey ranged from 20 to 300%. Kaczynski et al. (1973) discuss this point further.

Table 1 shows that epibenthic prey outnumbered planktonic prey by a factor of 8.5 at Dabob Bay and 6.4 at Anderson Island. This relation was reversed at Port Susan where feeding patterns were quite variable and the planktonic prey dominated.

Linear relationships between fish size (fork length) and number of prey found in the gut were not strong. Correlation coefficients for number on size were 0.39 for chum fry at Dabob Bay, 0.24 at Port Susan, and −0.03 at Anderson Island.

POTENTIAL PREY ABUNDANCE

The number of organisms per 0.5 m^2 captured by the pump technique and their numerical percent occurrence at Dabob Bay, Anderson Island, and Port Susan are given in Tables 2, 3, and 4, respectively. The data from Dabob Bay on May 21 shows a predictable decrease in abundance of organisms with increasing tide level as exposure time increases. At Dabob Bay the density of harpacticoid copepods decreased by three orders of magnitude during the study period (Table 2). The pump samples taken on April 21 were unfortunately taken at a high tide level and probably underestimate harpacticoid abundance. Harpacticoid densities at the Anderson Island site declined in a similar fashion from mid-April to the end of May (Table 3). No obvious trends of decrease were evident at Port Susan (Table 4). Prey density was considerably higher at Dabob Bay and Anderson Island than at Port Susan.

ELECTIVITY AND SIZE SELECTION

Ivlev electivity coefficients (E) were derived for the major prey items consumed in the three sampling areas. E values for harpacticoids, gammarid amphipods, and calanoid copepods are presented in Fig. 1. Chums fed selectively upon harpacticoids at Dabob Bay and to a lesser extent at Anderson Island. Avoidance or rejection of barnacle cyprids was evidenced by high negative values of E at all three locations. Insect and cladoceran electivities were high (> 0.9) at Port Susan.

A comparison of size-frequency distributions of total prey eaten and total prey available on specific sampling dates (Fig. 2) shows that the juvenile chums contained organisms at the lower end (0.4–1.5 mm) of the available size spectrum at Anderson Island and Dabob Bay. This trend is not as clear for the Port Susan chums because the pump did not sample many of the insects floating on the water's surface. The Mann-Whitney U test (Snedecor and Cochran 1956) was used to test the null hypothesis that there was no difference between the mean size of prey eaten and available. Data from the three areas were lumped ($N = 28$). Size selection did occur, as the null hypothesis was rejected at $P = 0.01$.

Since the salmon at Dabob Bay and Anderson Island were heavily selecting harpacticoids (Fig. 1), this prey item was chosen for additional analysis. Size-frequency diagrams for this fraction of the total prey spectrum are presented in Fig. 3. The Kolmogorov-Smirnov Two-sample Test (Tate and Clelland 1957) showed a highly significant difference ($P = 0.01$) between the size distributions of harpacticoids eaten and the harpacticoids available, except for April 21 (no difference), and May 21 at Dabob Bay ($P = 0.05$). Of the harpacticoids available, chums selected the smaller individuals.

TABLE 1. Total number and percentage composition (italics) of organisms consumed by juvenile chum salmon (*Oncorhynchus keta*) from three areas of Puget Sound, Washington, in 1971. Prey type in percent is given in the right-hand column.

	Calanoid	Harpacticoid	Euphausiid	Gammarid	Hyperiid	Insect	Insect larva	Cyprids	Barn. naup.	Invert. egg	Cumacean	Cladoceran	Zoea	Isopod	Larvacea	Polychaete	Gastropod	x̄ no./fish (SD)	x̄ Fork length (range) N = 6	% epibenthic	% planktonic	% other
Dabob Bay																						
Apr. 12	11	259	72	33	1	7	1			1								64.2	36.3 mm	*76.2*	*21.9*	*1.9*
	2.9	*67.3*	*18.7*	*8.6*	*0.3*	*1.8*	*0.3*			*0.3*								(43.6)	(33.0–39.0)			
Apr. 21	1	690	1	2		13		1										116.3	37.8 mm	*97.9*	*0.2*	*1.9*
	0.1	*97.5*	*0.1*	*0.3*		*1.8*		*0.1*										(43.1)	(35.5–43.0)			
Apr. 30	1	190	1	2		2	2	1										33.5	36.2 mm	*95.9*	*0.8*	*3.7*
	0.4	*94.5*	*0.4*	*1.0*		*1.0*	*1.0*	*0.4*										(20.8)	(35.0–38.5)			
May 10	12	2568	105	53	3	3		13		3	2	1					3	461.3	41.1 mm	*95.4*	*4.4*	*0.2*
	0.4	*92.9*	*3.8*	*1.9*	*0.1*	*0.1*		*0.4*		*0.1*	*0.1*	*0.1*					*0.1*	(189.4)	(36.5–48.5)			
May 21	59	1139	321	117	45	7	32	7	2								3	289.1	39.1 mm	*73.1*	*24.6*	*2.3*
	3.4	*65.9*	*18.5*	*6.8*	*2.6*	*0.4*	*1.9*	*0.4*	*0.1*								*0.1*	(116.1)	(35.5–42.0)			
x̄ no./fish	2.8	161.5	16.6	6.9	1.6	1.0	1.1	0.7	—	—	—	—					—	192.8		*87.7*	*10.3*	*2.0*
x̄%	*1.4*	*83.6*	*8.3*	*3.7*	*0.6*	*1.0*	*0.6*	*0.2*	—	—	—	—					—	(179.6)		*(12.0)*	*(11.9)*	*(1.2)*
(SD)	*(1.6)*	*(15.6)*	*(9.5)*	*(3.7)*	*(1.1)*	*(0.8)*	*(0.8)*	*(0.2)*	—	—	—	—					—					
Anderson Island																						
May 6	52	2325	45	4		5		3				2				2		406.3	42.3 mm	*95.6*	*4.0*	*0.4*
	2.1	*95.4*	*1.8*	*0.1*		*0.2*		*0.1*				*0.1*				*0.1*		(163.4)	(38.5–45.0)			
May 17	224	1069	63	6		1	1	13	3		2			2		1		230.8	45.7 mm	*78.7*	*20.9*	*0.4*
	16.2	*77.2*	*4.5*	*0.4*		*0.1*	*0.1*	*0.9*	*0.2*		*0.1*			*0.1*		*0.1*		(93.6)	(36.0–52.5)			
May 26	240	4825	663	50				11		1	2							965.3	42.5 mm	*84.5*	*15.5*	*0*
	4.1	*83.3*	*11.4*	*0.8*				*0.2*		*0.1*	*0.1*							(210.8)	(40.5–4.50)			
x̄ no./fish	28.6	456.6	42.8	3.3		0.3	—	1.5	—	—	—	—		—		—		534.1		*86.2*	*13.4*	*0.3*
x̄%	*7.4*	*85.3*	*5.9*	*0.4*		*0.1*	—	*0.4*	—	—	—	—		—		—		(383.5)		*(8.6)*	*(8.6)*	*(0.2)*
(SD)	*(7.6)*	*(9.2)*	*(4.9)*	*(0.4)*		*(0.1)*	—	*(0.4)*	—	—	—	—		—		—						
Port Susan																						
Apr. 13	18	2		6		167				1						1		32.5	37.5 mm	*4.6*	*9.2*	*86.1*
	9.2	*1.0*		*3.1*		*85.6*				*0.5*						*0.5*		(10.6)	(36.5–39.5)			
Apr. 23	15	6	2	49		36	6	12	2	47	3	53	1		4			39.5	37.9 mm	*49.3*	*32.3*	*17.7*
	6.3	*2.5*	*0.8*	*20.7*		*15.2*	*2.5*	*5.0*	*0.8*	*19.8*	*1.3*	*22.4*	*0.4*		*1.6*			(22.1)	(35.0–40.0)			
May 3	3	1		5		53	1	9			2	163						39.5	37.3 mm	*7.0*	*70.1*	*22.8*
	1.3	*0.4*		*2.1*		*22.4*	*0.4*	*3.7*			*0.8*	*68.8*						(53.9)	(36.5–38.0)			
May 12	6	8	88	11	2	51		20			4	190				1		63.5	41.0 mm	*11.2*	*75.0*	*13.6*
	1.6	*2.1*	*23.1*	*2.9*	*0.5*	*13.4*		*5.2*			*1.0*	*49.8*				*0.2*		(55.6)	(39.0–45.5)			
May 28	2	147	7	590		34	2	25		21		234						177.0	39.3 mm	*73.8*	*22.9*	*3.4*
	0.2	*13.8*	*0.7*	*55.6*		*3.2*	*0.2*	*2.4*		*2.0*		*22.0*						(74.4)	(37.0–43.5)			
x̄ no./fish	1.4	5.4	0.7	22.0	—	11.3	0.3	1.5	—	2.3	0.3	5.2	—		—	—		70.4		*29.2*	*41.9*	*28.7*
x̄%	*3.7*	*3.9*	*4.9*	*16.8*	—	*27.9*	*0.6*	*3.2*	—	*8.6*	*0.6*	*32.6*	—		—	—		(60.7)		*(30.8)*	*(29.2)*	*(32.8)*
(SD)	*(3.8)*	*(5.5)*	*(10.1)*	*(23.0)*	—	*(32.9)*	*(1.0)*	*(2.1)*	—	*(4.4)*	*(0.6)*	*(26.8)*	—		—	—						

TABLE 2. Occurrence (mean number ± 1 SD and percent) of organisms in epibenthic pump samples, Dabob Bay, 1971.

	Dabob Bay – 1971																			
Date	Apr. 12			Apr. 21			Apr. 30			May 10			May 21							
Water temp.	N/A			N/A			10.0 °C			N/A			13.3 C							
Tide level	+0.6 m			+1.8 m			+0.6 m			+0.1 m			+0.3 m	+0.4 m	+1.5 m	+1.6 m	+2.7 m	+3.0 m		
No. samples	3			3			2			2			1	1	1	1	1	1	Total	
	x̄ no.	SD	x̄%	x̄ no.	SD	x̄%	x̄ no.	SD	x̄%	x̄ no.	SD	x̄%	no.	no.	no.	no.	no.	no.	no.	%
Calanoid	115.0	122.7	*2.3*	33.3	14.5	*7.1*	3.5	11.0	*0.3*	2.0	1.0	*0.2*	6	1		8	4		19	*5.2*
Harpacticoid	935.6	739.9	*18.7*	16.3	5.0	*3.5*	506.6	250.0	*21.4*	97.3	102.6	*17.1*	4		1				5	*1.4*
Euphausiid	20.3	24.0	*0.4*	4.6	0.5	*1.0*	2.0	1.7	*0.1*	10.0	4.5	*0.9*		1					1	*0.3*
Gammarid[a]	893.6	500.2	*17.9*	14.3	10.9	*3.1*	1252	1879	*52.8*	554.0	394.7	*52.6*	125	105	1	8	2		241	*65.5*
Hyperiid	13.3	12.2	*0.3*																	
Insects				1.0	1.0	*0.2*	4.0	2.6	*0.2*						2	3	1		6	*1.6*
Cyprids	21.3	12.2	*0.4*	13.3	6.0	*2.9*	37.3	24.9	*1.6*	54.6	29.1	*5.2*	16	9	19	17		2	63	*17.1*
Barn. naup.	36.6	11.3	*0.7*							1.3	1.1	*0.2*								
Invert. egg	2820	1136	*56.5*	366.6	139.0	*78.5*	524.0	246.7	*22.1*	0.6	0.6	*0.1*								
Cumacean	3.3	4.1	*0.1*							4.0	2.0	*0.4*								
Isopod							6.6	4.9	*0.3*	1.3	1.1	*0.2*	11			7		1	19	*5.2*
Polychaete[b]	78.0	79.1	*1.6*	13.0	11.7	*2.9*	6.0	3.0	*0.3*	28.0	22.5	*2.7*	3						3	*0.8*
Gastropod[b]	37.3	33.3	*0.7*	4.0	1.0	*0.9*	20.6	8.9	*0.9*	200.0	136.1	*19.0*	2			1		1	4	*1.1*
Bivalve[b]							0.6	0.6	*0.1*											
Fish Egg															1		1	1	3	*0.8*
Ostracod										2.6	2.3	*0.3*								
Caprellid	21.3	24.4	*0.4*	0.6	0.6	*0.1*	2.6	1.5	*0.1*	14.6	10.2	*1.4*	2		1				3	*0.8*
Decapod													1						1	*0.3*
x̄ no./0.5 m²	4996	2342		467	165		2370	1032		1054	708		170	116	26	43	8	5	61	
x̄ no. unavailable	129			20			49			174			21	2	5	1	1	1	5	
%[c]	*2.58*			*4.28*			*2.06*			*16.50*									*8.19*	

[a] Several omitted from available prey category because of their large size.

[b] Omitted from available prey category because of burrowing habits or indigestibility (gastropods).

[c] Percentage of total organisms sampled that were designated as unavailable to the juvenile chum salmon.

TABLE 3. Occurrence (mean number ± 1 SD and percent) of organisms in epibenthic pump samples, Anderson Island, 1971. (See Table 2 footnotes.)

	Anderson Island — 1971													
Date	Apr. 5			Apr. 14			May 6		May 17			May 26		
Water temp.	8.8 C			8.3 C			9.4 C		11.7 C			10.0 C		
Tide level	+2.7 m			−0.2 m			+0.8 m		+1.1 m			+0.3 m		
No. samples	3			3			1		2			2		
	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%
Calanoid	26.0	3.0	*16.8*	178.6	145.8	*2.0*	36	*0.9*	10.0	1.4	*4.0*	49.5	12.0	*8.2*
Harpacticoid	4.0	1.0	*2.6*	4605	2176	*52.7*	3152	*79.4*	87.5	19.0	*34.6*	184.0	118.7	*30.5*
Euphausiid[a]				2.6	4.6	*0.1*			0.5	0.7	*0.2*	2.0	0	*0.3*
Gammarid[a]	13.0	7.9	*8.4*	714.6	308.0	*8.2*	379	*9.6*	28.5	0.7	*11.3*	164.0	93.3	*27.2*
Insects	0.6	0.6	*0.4*				1	*0.1*	0.5	0.7	*0.2*	1.5	0.7	*0.2*
Cyprids	15.3	4.0	*9.9*	3114	3213	*35.7*	275	*6.9*	87.0	28.2	*34.4*	62.0	31.1	*10.3*
Barn. naup.	69.0	10.1	*44.5*	21.3	24.4	*0.2*	24	*0.6*	1.0	0	*0.4*	0.5	0.7	*0.1*
Invert. egg	1.3	0.6	*0.9*				5	*0.1*	1.5	0.7	*0.6*	2.0	1.4	*0.3*
Cumacean									1.5	2.1	*0.6*	8.0	1.4	*1.3*
Zoea	2.0	1.0	*1.3*	10.6	12.2	*0.1*			1.5	0.7	*0.6*	4.0	1.4	*0.6*
Isopod[a]	21.0	19.3	*13.5*	13.3	9.2	*0.2*	35	*0.9*	29.0	33.9	*11.5*	6.0	1.4	*1.0*
Polychaete[b]	0.3	0.6	*0.2*	53.3	5.87	*0.6*	21	*0.5*	1.0	0	*0.4*	65.0	73.5	*10.8*
Gastropod[b]												1.5	0.7	*0.2*
Bivalve[b]	2.3	1.1	*0.9*									10.5	12.0	*1.7*
Fish Egg	1.0	1.0	*0.6*											
Ostracod				21.3	23.0	*0.2*	34	*0.9*	3.0	2.8	*1.2*	42.5	17.6	7.0
Mysis Larva									0.5	0.7	*0.2*			
$\bar{x}$ no./0.5 m^2	155	20		8739	3144		3968		253	20		603	341	
$\bar{x}$ no. unavailable	7.6			181			40		8			104		
%[c]	*4.90*			*2.07*			*1.00*		*3.16*			*17.24*		

TABLE 4. Occurrence (mean number ± 1 SD and percent) of organisms in epibenthic pump samples, Port Susan, 1971. Footnotes same as in Table 2.

	Port Susan — 1971														
Date	Apr. 13			Apr. 23			May 3			May 12			May 28		
Water temp.	N/A			10.0 C			N/A			14.4 C			16.7 C		
Tide level	+0.8 m			+3.0 m			+1.8 m			+0.1 m			−0.1 m		
No. samples	3			2			2			2			2		
	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%	$\bar{x}$ no.	SD	$\bar{x}$%
Calanoid	17.0	17.0	*5.4*	11.0	9.9	*5.8*	32.0	29.6	*21.9*	46.0	29.7	*4.2*	1.5	0.7	*0.5*
Harpacticoid	50.0	14.7	*15.9*	1.5	2.1	*0.7*	1.0	0	*0.7*	301.5	166.1	*27.8*	28.0	7.0	*10.0*
Euphausiid[a]				1.0	1.4	*0.5*	64.0	83.4	*43.8*	79.0	59.4	*7.3*			
Gammarid[a]	98.6	38.0	*31.5*	0.5	0.7	*0.3*	8.0	4.2	*5.5*	541.0	420.0	*49.9*	38.5	3.5	*13.8*
Insects	3.0	2.0	*0.9*				2.0	1.4	*1.4*	0.5	0.7	*0.1*			
Cyprids	97.6	16.0	*31.1*	166.5	137.8	*87.6*	29.0	9.9	*19.9*	34.5	21.9	*3.2*	51.5	10.6	*18.4*
Barn. naup.	1.3	0.5	*0.4*	1.5	2.1	*0.7*	1.5	0.7	*1.0*	0.5	0.7	*0.1*			
Invert. egg	2.3	1.1	*0.7*				5.0	7.0	*3.4*	35.5	16.2	*3.3*	36.5	21.9	*13.1*
Cumacean	10.6	2.3	*3.4*				1.0	0	*0.7*	6.5	0.7	*0.6*	57.0	4.2	*20.4*
Zoea	0.6	0.6	*0.2*	1.0	0	*0.5*	0.5	0.7	*0.3*						
Isopod[a]	9.3	10.1	*3.0*							3.5	2.1	*0.3*			
Polychaete[b]	4.0	3.4	*1.3*				2.0	0	*1.4*	4.5	0.7	*0.4*	31.0	4.2	*11.1*
Gastropod[b]										1.5	2.1	*0.1*			
Bivalve[b]	2.6	3.0	*0.9*												
Fish Egg	13.3	18.9	*4.3*	2.0	0	*1.1*				1.0	0	*0.1*			
Ostracod	3.0	1.0	*1.0*							16.0	15.5	*1.5*	33.5	6.3	*12.0*
Medusae													1.0	1.4	*0.4*
Cladoceran				5.0	7.0	*2.6*							1.0	1.4	*0.4*
$\bar{x}$ no./0.5 m^2	313	33		190	155		151	127		1084	589		280	40	
$\bar{x}$ no. unavailable	8			0			3			17			70		
%[c]	*2.55*			*0*			*1.98*			*1.56*			*25.00*		

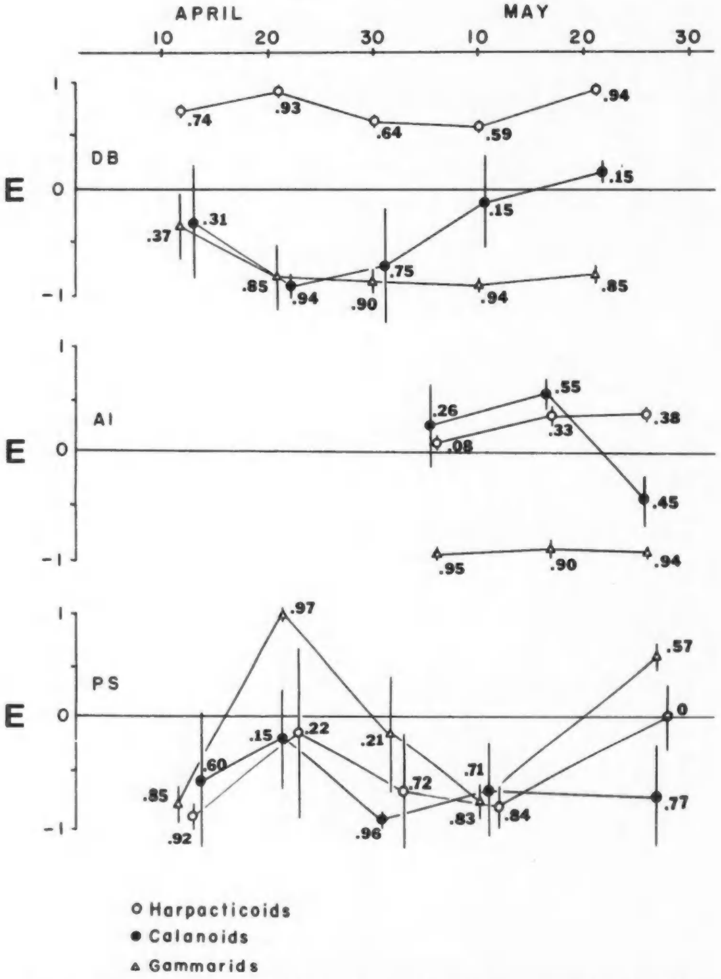


FIG. 1. Ivlev electivity coefficients (± 1 SD) of select prey for juvenile chum salmon (*Oncorhynchus keta*) by date and location in Puget Sound, 1971. Positive values of E indicate selection, negative values indicate avoidance, and a value of zero indicates that prey were taken in proportion to their abundance.

Discussion

The conclusion that size selective feeding did occur depends heavily upon the assumption that the fish were feeding on items similar to those sampled by the pump. Such an assumption is tenable for several reasons. First, the types of organisms found in the fish stomachs (Table 1) are clearly the same as those found in the pump samples (Tables 2, 3, and 4), with the exception of the terrestrial and marine insects at Port Susan. Secondly, Kaczynski et al. (1973) found little resemblance between stomach contents of chum salmon and the contents of Clarke–Bumpus plankton tows taken in the same shallow water where the fish feed during the day. Thirdly, several personal observations of young salmon feeding in the same areas as were sampled with the pump have been made from the beaches,

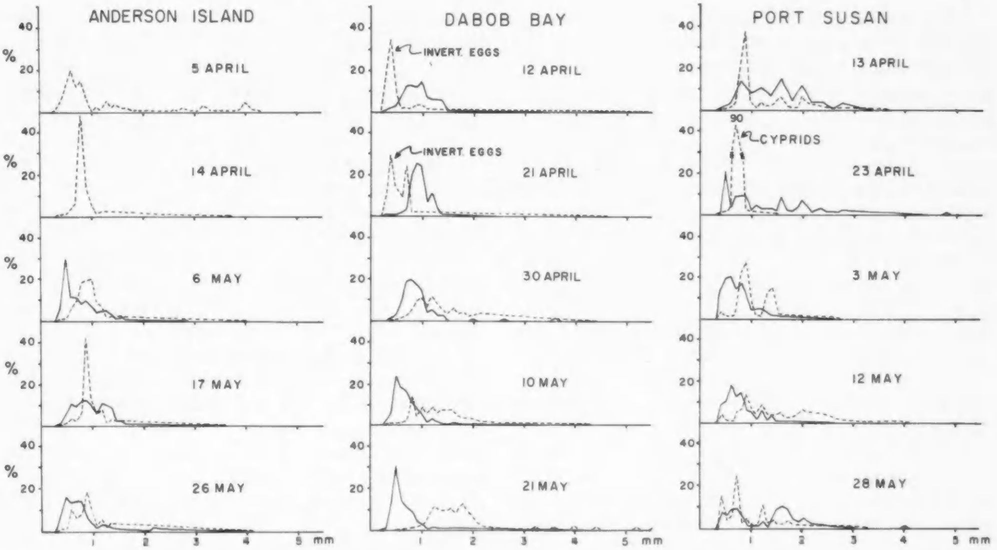


FIG. 2. Size-frequency distributions (as percent) of total prey in the diet of juvenile chum salmon (solid line) and in pump samples (dashed line) by location. No fish were found on April 5 and 14 at Anderson Island.

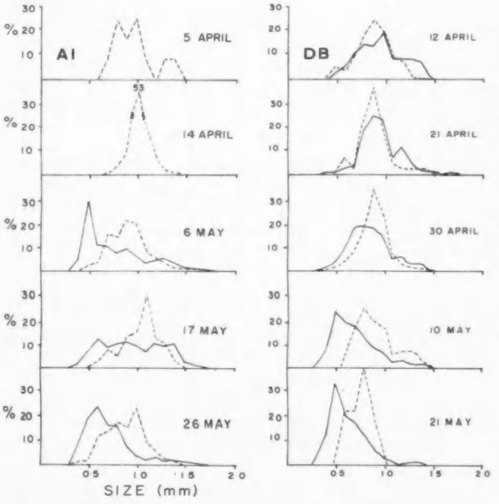


FIG. 3. Size-frequency distributions (as percent) of harpacticoid copepods found in the stomachs of juvenile chum salmon (solid line) and in pump samples (dashed line) from two areas of Puget Sound, 1971. No fish were found on April 5 and 14 at Anderson Island.

further substantiating the validity of the original assumption.

The sample size (N = 6) of fish chosen for this study may appear to be small. Examination of six fish per date adequately described the diet when the dominant prey item was harpacticoids. Since the coefficients of variation for these prey were so consistently low in comparison to coefficients derived for other prey items, it was not cost-effective to examine additional fish. A larger sample size of fish from the Port Susan area would have been desirable, however, because of the greater breadth of diet there.

The mesh size of the pump straining net might appear to introduce error. If the mesh allowed very small organisms to pass through, the size-frequency distributions would be skewed toward the larger sized organisms. The smallest intact prey found in any of the 78 fish examined was 0.4 mm in length, and the pump mesh used retained many organisms 0.3 mm in length and often much smaller crustacean nauplii, tending to discount any mechanical sampling bias. In addition, the length of the straining net was very long relative to the net's diameter and pump flow, minimizing pressures that might force small organisms through the net.

A more difficult problem is that of knowing whether all organisms sampled by the pump are equally available as prey. Some prey may be more available than others. For instance, the gammarid amphipods are much more motile than harpacticoids and thus may be more difficult to capture. The larger organisms probably are more able to escape capture by having a speed advantage over the smaller ones. However, several relatively large, fast-swimming prey were found in the guts of several fish. For example, gammarids up to 4.4 mm long, euphausiids up to 4.8 mm in length, and calanoid copepods 3.2 mm long (*Calanus* sp.) occurred in some fish, but usually no more than two or three of these larger prey were found in any one fish. The large calanoids in the guts were found with the antennae folded back alongside the body, implying that they were swallowed head first. The largest intact organism found in all the fish was a polychaete 8.0 mm long. The observed preference for epibenthic harpacticoids exhibited by the Dabob Bay and Anderson Island chum salmon may then reflect selection not purely on the basis of size, but rather an apparent selection due to the greater availability of the harpacticoids in relation to other prey.

The observed reductions in harpacticoid abundance (Tables 2 and 3) could have been due to intense predation by the juvenile chum salmon or to natural seasonal fluctuations in abundance of the prey populations. Neither of these alternatives could be confirmed by this study; however, the former alternative is suggested by the large numbers of harpacticoids eaten per fish at both sites during May (Table 1) and by the high numbers of fish present in the study areas at that time. Recruitment of recently hatched chum to the intertidal beaches of Puget Sound typically begins in early or mid-April and lasts until mid-June. Fish densities estimated by visual counts reached their peak in mid-May, with 3800/km at Dabob Bay, 3700/km at Anderson Island, and 5800/km in Port Susan (data courtesy Washington State Department of Fisheries).

Selective feeding by a variety of juvenile fish is well documented in the literature (Blaxter 1965; Brooks 1968; LeBrasseur 1969; Parsons and LeBrasseur 1970; Rosenthal and Hempel 1970). Okada and Taniguchi (1971) found that inshore populations of juvenile pink and chum salmon rapidly changed the size (width) of prey taken when the fish reached a length of 55 mm, so that larger fish sought larger prey, almost all of which were planktonic. In contrast to the findings of the studies mentioned above, the selection for the smaller of the total prey available and for the smaller of the major prey item (the harpacticoids) found in this study is noteworthy. Perhaps chum fry use a different foraging strategy when feeding on epibenthic prey than when feeding on planktonic prey, but this cannot be confirmed without further work.

Both pink and chum salmon juveniles school together during even-numbered years in the study areas; in the odd-numbered years, only juvenile chum salmon are found. A comparison (signed-rank test) of paired observations on the mean lengths of the various prey found eaten in 1970 (pink versus chum on specific sampling dates, reported in part by Kaczynski et al. 1973) showed no significant difference in size of prey consumed by the young pink and chum ($P = 0.16$). Kaczynski et al (1973) found true behavioral differences in prey selection between the juvenile pinks and chums. It is possible that prey size selection also plays a part in trophic separation of these two species, and if niche partitioning via prey size is taking place, then the finding of selection for smaller prey by chum salmon would not be quite so surprising a result.

Acknowledgments

We express our sincere gratitude to Mr R. J. Gerke and the Washington State Department of Fisheries for their assistance in providing sampling equipment and for taking samples used in this study. This report was submitted in partial fulfillment of the requirements for a nonthesis Master of Science degree by the senior author. Funding was provided by U.S. Atomic Energy Commission Contract AT(45-1)-2225 TA26-27.

BLAXTER, J. H. S. 1965. The feeding of herring larvae and their ecology in relation to feeding. Calif. Coop. Oceanic Fish. Invest. Rep. 10: 79–88.

BROOKS, J. L. 1968. The effects of prey size selection by lake planktivores. Syst. Zool. 17: 273–291.

BROOKS, J. L., AND S. I. DODSON. 1965. Predation, body size, and composition of plankton. Science (Wash. D.C.) 150: 28–35.

FOSKETT, D. R. 1951. Young salmon in the Nanaimo area. Fish. Res. Board Can. Pac. Prog. Rep. 86: 18–19.

GILHOUSEN, P. 1962. Marine factors affecting the survival of Fraser River pink salmon, p. 105–111. *In* Symposium on Pink Salmon. H. R. MacMillan Lectures in Fisheries, Univ. British Columbia, Vancouver, B.C., 1960.

IVLEV, V. S. 1961. Experimental ecology of the feeding of fishes. Yale Univ. Press, New Haven and London. 302 p. (Transl. from Russian by D. Scott)

KACZYNSKI, V. W., R. J. FELLER, J. CLAYTON, AND R. J. GERKE. 1973. Trophic analysis of juvenile pink and chum salmon (*Oncorhynchus gorbuscha* and *O. keta*) in Puget Sound. J. Fish. Res. Board Can. 30: 1003–1008.

KIRKWOOD, J. B. 1962. Inshore-marine and freshwater life history of the pink salmon, *Oncorhynchus gorbuscha* (Walbaum), and the chum salmon, *O. keta* (Walbaum), in Prince William Sound, Alaska. Ph.D. Thesis. Univ. Louisville, Ky. 300 p.

LEBRASSEUR, R. J. 1969. Growth of juvenile chum salmon (*Oncorhynchus keta*) under different feeding regimes. J. Fish. Res. Board Can. 26: 1631–1645.

LEBRASSEUR, R. J., AND R. R. PARKER. 1964. Growth rate of central British Columbia pink salmon. J. Fish. Res. Board Can. 21: 1101–1128.

MANZER, J. I. 1956. Distribution and movement of young Pacific salmon during early ocean residence. Fish. Res. Board Can. Pac. Prog. Rep. 106: 24–28.

1969. Stomach contents of juvenile Pacific salmon in Chatham Sound and adjacent waters. J. Fish. Res. Board Can. 26: 2219–2223.

MERRELL, T. R. 1970. Alaska's fishery resources – the chum salmon. U.S. Fish. Wildl. Serv. Bur. Commer. Fish. Leafl. Fish. 632, 7 p.

OKADA, S., AND A. TANIGUCHI. 1971. Size relationship between salmon juveniles in shore waters and their prey animals. Bull. Fac. Fish., Hokkaido Univ. 22: 30–36.

PARSONS, T. R., AND R. J. LEBRASSEUR. 1970. The availability of food to different trophic levels in the marine food chain, p. 325–343. *In* J. H. Steele [ed.] Marine Food Chains. Oliver and Boyd, Edinburgh.

ROSENTHAL, H., AND G. HEMPEL. 1970. Experimental studies in feeding and food requirements of herring larvae (*Clupea harengus* L.), p. 344–364. *In* J. H. Steele [ed.] Marine Food Chains. Oliver and Boyd, Edinburgh.

SNEDECOR, G. W., AND W. G. COCHRAN. 1956. Statistical methods. Iowa State Univ. Press, Ames, Iowa. 593 p.

TATE, M. W., AND R. C. CLELLAND. 1957. Nonparametric and shortcut statistics in the social, biological, and medical sciences. Interstate Printers and Publishers, Inc. 171 p.

Cholesterol Requirements of Juvenile American Lobster (*Homarus americanus*)

JOHN D. CASTELL, EDGAR G. MASON, AND JANE F. COVEY

Department of the Environment, Fisheries and Marine Service, Halifax Laboratory, Halifax, N.S. B3J 2R3

CASTELL, J. D., E. G. MASON, AND J. F. COVEY. 1975. Cholesterol requirements of juvenile American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 32: 1431–1435.

In preliminary feeding trials with juvenile American lobsters (*Homarus americanus*) there were some differences in growth and survival that appeared to be related to deletion or addition of cod liver oil, mineral salts, vitamins, and glucosamine. However, the results were questionable due to deficiency of dietary cholesterol. Only when 1% cholesterol was added to the control diet was growth and survival achieved similar to that of lobsters fed brine shrimp. The optimum or required level of cholesterol was found to be approximately 0.5% of the dry weight of the diet.

CASTELL, J. D., E. G. MASON, AND J. F. COVEY. 1975. Cholesterol requirements of juvenile American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 32: 1431–1435.

Lors d'essais préliminaires d'alimentation de jeunes homards américains (*Homarus americanus*), il y avait dans la croissance et la survie, des différences qui semblaient liées à la suppression ou à l'addition d'huile de foie de morue, de sels minéraux, de vitamines et de glucosamine. Les résultats sont douteux, à cause du manque de cholestérol dans le régime. Ce n'est qu'après addition de 1% de cholestérol au régime témoin que la croissance et la survie atteignent le même niveau que chez les homards nourris d'artémies. Le niveau optimal ou requis de cholestérol se situe aux environs de 0.5% du poids sec du régime.

Received November 1, 1974
Accepted March 19, 1975

Reçu le 1 novembre 1974
Accepté le 19 mars 1975

THE control purified (artificial) diet used for adult lobsters, (*Homarus americanus*, Castell and Budson 1974) has been found to be unsatisfactory for juvenile lobsters. Fifth stage lobsters would not survive beyond the 10th molt when fed artificial diets of the formula reported for adults. It was discovered that cod liver oil, used as the lipid source in the control diet, was deficient in cholesterol.

It has been shown that some marine decapods require dietary cholesterol (Kanazawa et al. 1971a, b; Shudo et al. 1971). Though it has been reported that another species of lobster, *Panulirus japonica* was unable to synthesize cholesterol de novo (Teshima and Kanazawa 1971b), this paper is the first qualitative and quantitative report of a dietary sterol requirement of *Homarus americanus.*

In our preliminary feeding trials it was observed that preventing juveniles from consuming their cast shells increased mortalities. As the cast shell apparently plays a significant role in survival of young lobsters, it was thought that calcium, phosphorus, glucosamine, or extracted lobster shell lipid might affect growth and survival of juveniles. Kitabayashi et al. 1971 have reported that dietary supplementation with calcium, phosphorus, and glucosamine enhanced growth of the Kuruma prawn.

In an attempt to develop a control artificial diet suitable for nutrition studies with juvenile lobsters, a number of dietary factors were tested and compared with brine shrimp (*Artemia salina*) control diet and a starvation regimen.

Materials and Methods

Gravid female lobsters weighing 500 g–1 kg were captured locally. Larval lobsters were obtained by placing a gravid female in a 36-liter fiberglass aquarium equipped with a special nylon-mesh bottomed, overflow trap and supplied with filtered sea water at 20 C. The larvae were held in 22-liter conical fiberglass aquaria, in 20 C constant flowing filtered sea water. After they reached the 4th stage, the lobsters were placed in trays with individual compartments. All juveniles were fed frozen adult brine shrimp from hatching until commencement of feeding trials. Artificial diets were modified by adding or deleting cod liver oil, cholesterol, mineral salts, vitamins, and glucosamine.

As the cholesterol deficiency appeared to be a critical factor in the artificial diets, we subsequently determined the required dietary level of this compound for juvenile lobsters. This involved feeding

Printed in Canada (J3607)
Imprimé au Canada (J3607)

TABLE 1. Percentage composition of artificial diets used in juvenile nutrition studies.

Ingredient	Diet no.												
	1	2	3	4	5	6	7	8	9	10	11	12	13
Casein (Vitamin free)	50	50	50	50	50	50	50	50	BRINE SHRIMP	STARVED	50	50	50
Gelatin	10	10	10	10	10	10	10	10			10	10	10
α-cellulose	20.8	18.8	13.8	18.8	18.8	28.8	18.8	21.8			18.8	18.8	18.8
Corn starch	5	5	5	5	5	5	5	5			5	5	5
Mineral mix[a]	3	3	3	3	3	3	3	—			3	3	3
Vitamin mix[a]	—	2	2	2	2	2	2	2			2	2	2
Choline chloride (30%)	1	1	1	1	1	1	1	1			1	1	1
Vitamin E acetate	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2			0.2	0.2	0.2
Cod liver oil	10	10	10	—	9	—	9	10			—	—	—
Ethyl esters of[b] Cod liver oil F.A.	—	—	—	10	—	—	—	—			9.5	9	8
Cholesterol	—	—	—	—	1	—	—	—			0.5	1.0	2.0
Glucosamine	—	—	5	—	—	—	—	—			—	—	—
Lobster Shell Oil[c]	—	—	—	—	—	—	1	—			—	—	—

[a] As listed by Castell and Budson 1974.

[b] Prepared by Nu Check Prep., Elysian, Minnesota.

[c] Oil extracted from shell wastes obtained from commercial lobster processing plant.

diets containing 0, 0.5, 1.0, and 2.0% of the dry weight as cholesterol (Diets 4, 11, 12, and 13, respectively), and using cod liver oil ethyl esters as the lipid source; no sterols other than cholesterol were added. The compositions are given in Table 1. All ingredients were purchased from Nutritional Biochemicals Co., except where stated otherwise. The diets were prepared by mixing dry ingredients (40%) with boiling water (60%) and placed in a refrigerator to allow the gelatin to set. The moist food was then extruded through a sodium wire extruder forming a spaghetti-like fiber 1.5 mm in diameter. The food was cut into pieces approximately 4 mm in length and frozen in plastic bags until fed to the lobsters.

In the preliminary feeding trials Diets 1 through 10 were fed to groups of 20 juvenile lobsters. Each group of juveniles was housed in two separate plastic trays, each with 10 individual compartments 10 × 10 × 5 cm. Each group of lobsters was selected to have the same average initial weight (7.60 g) and average initial age (60 days). The age ranged from 40 to 210 days and weights from 0.1 to 4 g.

In the cholesterol level study triplicate groups of 10 juveniles were used for each of Diets 4, 11, 12, and 13. The 120 lobsters, all from the same hatch, were 153 days old at the start of the experiment and weighed an average of 0.84 g.

In all feeding experiments the lobsters were fed ad lib., with fresh food added daily at approximately 0900 and 1600. Uneaten food and fecal waste were removed each day before the morning feeding. The lobsters were weighed every 2 wk and the lobsters that molted were noted every day at feeding time. At termination of the cholesterol level study, lipid content of the whole lobster was estimated by the Bligh and Dyer (1959) chloroform–methanol extraction procedure. Samples of two or three lobsters (total weight 2–5 g) were combined to give a large enough sample for accurate analysis and homogenized for lipid extraction. The proportion of neutral lipid to phospholipid was determined by chromatography on acid-washed Florisil® (Carrol 1964) using chloroform and methanol, respectively, as eluting solvents. The cholesterol content of the neutral lipid was estimated by the perchloric acid–phosphoric acid–ferric chloride procedure of Momose et al. 1963.

The percent dry weight of juvenile lobsters was determined by difference after drying at 110 C for 24 h.

Results

In the preliminary feeding trials with Diets 1–10, the number of molts in the groups receiving Diet 5 (1% cholesterol) and Diet 9 (frozen brine shrimp) was significantly higher than in any other group (Table 2). The high number of molts in these two groups was reflected in increased survival and was not due to the average molt interval which did not differ significantly among the 10 groups.

Diets 6 (fat free) and 10 (starvation) resulted in the poorest growth rate (Fig. 1A) and the highest mortality (Table 2). Figures 1A and B show that only lobsters receiving the artificial diet with 1% cholesterol added (Diet 5) or the diet of brine shrimp continued to gain weight after 24 days feeding. Cod liver oil has less than 1% cholesterol (Brocklesby 1940), and thus when cod liver oil was included at 10% of the dry weight of the diet, lobsters were receiving less than 0.1% cholesterol. Analysis showed that oil extracted from adult lobster shell wastes contained about 12% cholesterol. Therefore, the

TABLE 2. Molt and mortality data for preliminary diet trials with juvenile American lobsters (*Homarus americanus*), 20 lobsters per diet.

Diet	No. of molts per 20 animals over 95 day trial	Average molt interval (days)	Average interval from last molt to death (days)	Mortality no. of lobsters	Avg. no. molts per lobster
1	36	25.2	28.9	16	1.8
2	39	27.8	17.8	16	1.85
3	43	26.8	18.5	15	2.15
4	35	25.0	26.9	16	1.75
5	63	23.4	16.3	4	3.15
6	28	22.0	41.2	18	1.4
7	34	29.1	34.1	17	1.7
8	34	27.9	29.2	17	1.7
9	51	26.9	15.0	1	2.55
10	20	21.9	50.6	20	1.0

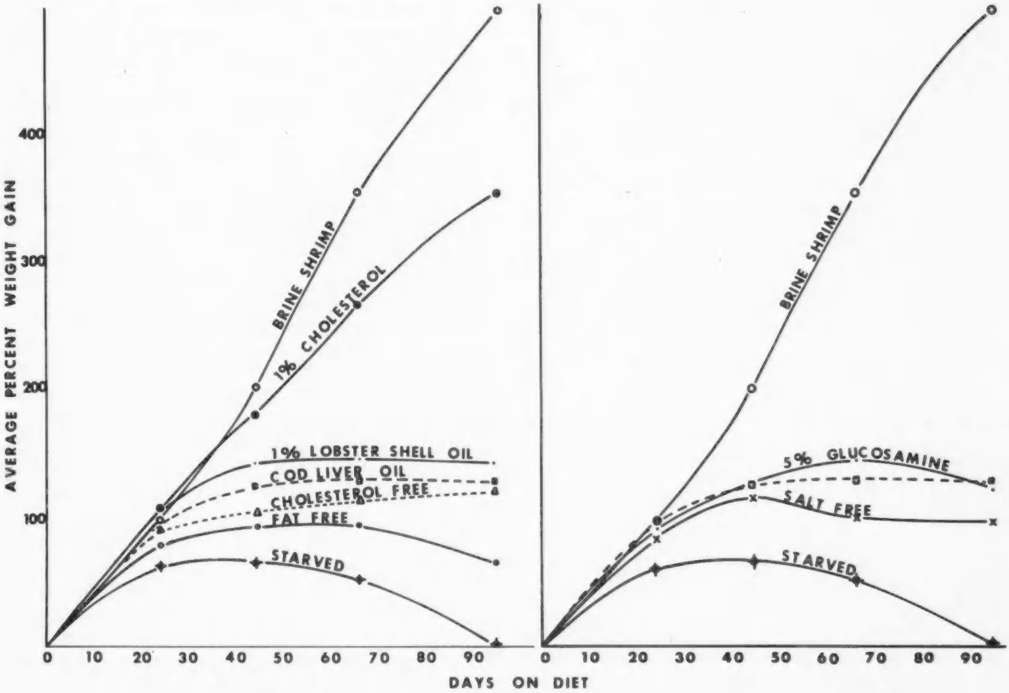


FIG. 1. The effect of (A) several dietary lipids and (B) glucosamine supplementation and mineral salt deficiencies on growth of juvenile American lobsters (*Homarus americanus*) compared with unfed and brine shrimp fed controls. Average initial age (60 days) and weight (0.38 g).

lobsters receiving Diet 7 with 1% lobster shell oil and 9% cod liver oil were receiving about 0.2% cholesterol, which might explain the slightly better growth of lobsters receiving this diet (Fig. 1A). The lobsters receiving the cholesterol free diet (4) grew slightly less rapidly than those on 10% cod liver oil (0.1% cholesterol). Analysis of the frozen brine shrimp (*Artemia salina*) yielded 90% moisture and 1.65% lipid; 12.3% of the lipid was cholesterol.

All diets except brine shrimp (Diet 9) and the diet incorporating 1% cholesterol (Diet 5) were deficient in cholesterol, and therefore the nutritional evaluation of other dietary ingredients was doubtful. Growth (Fig. 1B) and mortality (Table 2) of lobsters receiving the glucosamine supplemented diet (3) was not significantly different from cod liver oil control diet fed lobsters. Deleting salt mix (Diet 8) resulted in suppressed growth after 45 days (Fig. 2) and slightly higher mortality by 95 days. Had these diets (3 and 8) not been deficient in cholesterol, addition of glucosamine and deletion of salt might have exerted a more significant influence.

The growth and mortality figures for Diet 1 (vitamin free) were not significantly different from those for Diet 2 (cod liver oil control) and thus are not indicated in Fig. 1. It can be seen in Fig. 2, that the optimum growth was achieved with 0.5% cholesterol, and that 2.0% cholesterol resulted in some repression of growth. The 0.5% cholesterol diet also resulted in the highest incidence of molt and the lowest mortality.

The mean percent dry weight of Diet 11 (0.5% cholesterol) lobsters (21.5 ± 3.7%) was higher than that of the animals receiving the other diets (16.4–18.0%). (Difference significant only at 10% level.)

The lipid content of juvenile lobsters (0.7–1.1%; Table 4) is similar to that reported by Idler and Wiseman (1971) for adult lobsters (0.81%) and sterol values are also similar (90 mg % for adult lobsters). The number of survivors on Diet 4 was very small and thus only two lipid extractions were possible. There was no significant difference in the cholesterol content of juveniles receiving Diets 11 and 12. Surprisingly, lobsters receiving 2% cholesterol retained less cholesterol than those receiving 0.5 and 1.0%. This suggests that excess dietary cholesterol induces a mechanism in the lobster for cholesterol elimination resulting in a lower body content of this sterol than that obtained with optimal dietary levels.

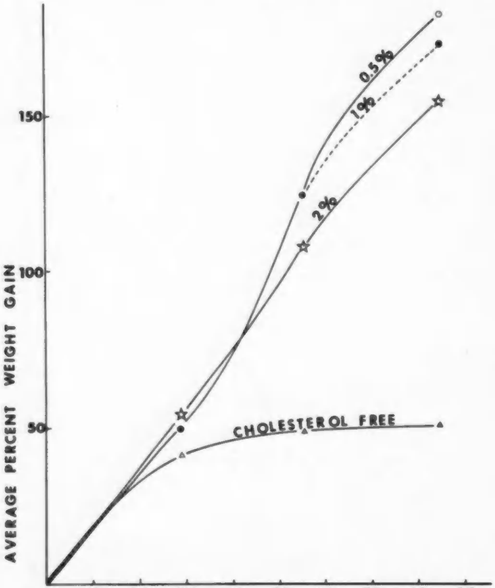


FIG. 2. Growth curves for dietary cholesterol level study. The average number of molts per lobster was 2.07, 3.40, 3.03, and 3.23 and average mortality was 70, 6.7, 30, and 10.0% for cholesterol free and 0.5, 1.0, and 2.0% cholesterol groups, respectively.

Discussion

The results of these experiments show quite clearly that for maximum weight gain and survival, juvenile lobsters require a dietary source of sterol such as cholesterol. The required dietary level is approximately 0.5% of the dry weight of the diet. This is the same level as Kanazawa et al. (1971) found for the prawn *Penaeus japonicus*. Teshima (1972) and Teshima and Kanazawa (1971b) have also reported that the lobster *Panulirus japonica*, the crab *Portunus trituberculatus*, and brine shrimp *Artemia salina* require dietary sterol. It was, thus, not surprising to find that the American lobster (*Homarus americanus*) required a dietary source of sterol. It appears, in fact, that crustaceans and insects in general are unable to synthesize cholesterol (or other sterols) from acetate and/or mevalonate. Zandee (1962, 1967) reported on the absence of a mechanism for synthesizing cholesterol from C^{14} labeled acetate in a number of crustaceans. Though marine crustaceans do not have a mechanism for de novo synthesis of sterols, they are able to alter dietary sterols to meet their demand for specific sterols (Kanazawa and Teshima 1971a, b, c; Teshima 1971, 1972). Further investigation is necessary for a complete understanding of the requirement for metabolic function of cholesterol and other sterols in lobsters and other crustaceans.

Though it was not surprising to find that American lobsters, like many other crustaceans, require a dietary source of sterol, it was important to demonstrate this and to determine the required level. Many marine fish oils, like cod liver oil, have insufficient sterol to meet the needs of the lobster. A diet of cod fish alone would not be satisfactory for lobster culture.

We were able to maintain some juveniles on the 1% cholesterol diet for greater than 10 mo with very low mortality. The major deficiency in the test diet used by Castell and Budson (1974) was insufficient cholesterol. This development of a maintenance diet now permits us to investigate other nutritional factors such as essential amino acids, vitamins, essential fatty acids, and minerals.

AUDOIN, J., AND M. LEGLISE. 1972. Techniques for raising lobster larvae. Int. Counc. Explor. Sea, Shellfish and Benthos Committee, C.M. 1972/Ki 41.

BAILEY, B. E. 1952. Marine oils with particular reference to those of Canada. Bull. Fish. Res. Board Can. 89: p. 86 and 335.

BLIGH, E. G., AND W. J. DYER. 1959. A rapid method of total lipid extraction and purification. Can. J. Biochem. Physiol. 37: 911–927.

CARROL, K. K. 1964. Acid-treated florisil as an adsorbent for column chromatography. J. Am. Oil Chem. Soc. 40: 413–419.

CASTELL, J. D., AND S. D. BUDSON. 1974. Lobster nutrition: the effect on *Homarus americanus* of dietary protein levels. J. Fish. Res. Board Can. 31: 1363–1370.

GUARY, J-C. B., AND A. KANAZAWA. 1973. Distribution and fate of exogenous cholesterol during the molting cycle of the prawn *Penaeus japonicus*. Comp. Biochem. Physiol. 46A: 5–10.

IDLER, D. R., AND P. WISEMAN. 1971. Sterols of crustaceans. Int. J. Biochem. 2(7): 91–98.

KANAZAWA, A., M. SHIMAYA, M. KAWASAKI, AND M. KASHIWADA. 1970. Nutritional requirements of prawn — I. Feeding an artificial diet. Bull. Jap. Soc. Sci. Fish. 36: 949–954.

KANAZAWA, A., N. TANAKA, S. TESHIMA, AND K. KASHIWADA. 1971a. Nutritional requirements of prawn — II. Requirement for sterols. Bull. Jap. Soc. Sci. Fish. 37: 211–215.

1971b. Nutritional requirements of prawn — III. Utilization of the dietary sterols. Bull. Jap. Soc. Sci. Fish. 37: 1015–1019.

KANAZAWA, A., AND S. TESHIMA. 1971c. *In vivo* conversion of cholesterol to steroid hormones in the spiny lobster, *Panulirus japonica*. Bull. Jap. Soc. Sci. Fish. 37: 891–896.

KITABAYASHI, K., H. KARATA, K. SHUDO, K. MAKAMURA, AND S. ISHIKAWA. 1971. Studies on formula feed for Kurama Prawn — I. On the relationship among glucosamine, phosphorous and calcium. Bull. Tokai Reg. Fish. Res. Lab., Tokyo. 65: 91–108. (Translated by Division of Foreign Fisheries (Translations), National Marine Fisheries, NOAA, Dep. Commerce.)

MOMOSE, T., Y. UEDA, K. YAMAMOTO, T. MASUMURA, AND K. OHTA. 1963. Determination of total cholesterol in blood serum with perchloric acid–phosphoric acid–ferric chloride reagent. Anal. Chem. 35: 1752–1753.

SHUDO, K., K. NAKAMURA, S. I. SHIKAWA, AND K. KITABAYASHI. 1971. Studies on formularion feed for Kuruma prawn — V. On the growth-promoting effects of both squid liver oil and cholesterol. Bull. Tokai Reg. Fish. Res. Lab., Tokyo. 65: 129–138.

TESHIMA, Ș. 1971. Bioconversion of β-sitosterol and 24-methyl-cholysterol to cholesterol in marine crustacea. Comp. Biochem. Physiol. 39B: 815–822.

1972. Studies on the sterol metabolism in marine crustaceans. Mem. Fac. Fish., Kagoshima Univ., 21(2): 69–147.

TESHIMA, S., AND A. KANAZAWA. 1971a. Utilization and biosynthesis of sterols in *Artemia salina*. Bull. Jap. Soc. Sci. Fish. 37: 720–723.

1971b. Biosynthesis of sterols in the lobster, *Panulirus japonica*, the prawn *Penaeus japonicus*, and the crab *Portunus trituberculatus*. Comp. Biochem. Physiol. 38B: 597–602.

ZANDEE, D. I. 1962. Lipid metabolism in *Asticus asticus* (L). Nature 195: 814–819.

1967. Absence of cholesterol synthesis as contrasted with the presence of fatty acid synthesis in some arthropods. Comp. Biochem. Physiol. 20: 811–822.

NOTES

Possible Interference in the Isolation of IPN Virus from Carrier Fish

BRUCE L. NICHOLSON

Department of Microbiology and Migratory Fish Research Institute, University of Maine, Orono, Me. 04473, USA

AND ROGER DEXTER

U.S. Bureau of Sport Fisheries and Wildlife, Craig Brook National Fish Hatchery, East Orland, Me., USA

NICHOLSON, B. L., AND R. DEXTER. 1975. Possible interference in the isolation of IPN virus from carrier fish. J. Fish. Res. Board Can. 32: 1437–1439.

This report describes an instance of possible homologous viral interference in the isolation of IPN virus from carrier fish. Brook trout (*Salvelinus fontinalis*), suspected of being carriers of IPN virus, were examined for the presence of the virus by inoculating monolayer cultures of RTG-2 cells with different dilutions of tissue homogenates of the suspected fish. Cultures of RTG-2 cells infected with concentrated tissue homogenates exhibited little, if any, cytopathic effect (CPE) and yielded little infectious IPN virus at 72 h after infection. However, cell cultures infected with a relatively high dilution of tissue homogenate exhibited extensive CPE and resulted in high yields of infectious virus.

NICHOLSON, B. L., AND R. DEXTER. 1975. Possible interference in the isolation of IPN virus from carrier fish. J. Fish. Res. Board Can. 32: 1437–1439.

Nous décrivons dans cet article un cas d'interférence possible par un virus homologue dans l'isolation du virus de la pancréatite infectieuse nécrosante (PIN) de poissons porteurs. Des ombles de fontaine (*Salvelinus fontinalis*), soupçonnés d'être porteurs du virus de la PIN, furent examinés en vue de déceler la présence du virus, en inoculant des cultures monocellulaires de cellules de RTG-2 avec différentes dilutions d'homogénats tissulaires de poissons suspects. Les cultures de cellules RTG-2 infectées d'homogénats tissulaires concentrés ne montrent que peu, si tant est qu'elles en montrent du tout, d'effet cytopathique (ECP) et ne produisent que peu de virus de PIN 72 h après infection. Cependant, les cultures cellulaires infectées par une dilution relativement forte d'homogénat tissulaire montrent un ECP prononcé et donnent de forts rendements en virus infectieux.

Received December 16, 1974
Accepted March 20, 1975

Reçu le 16 décembre 1974
Accepté le 20 mars 1975

WITH the increased interest in fish culture and the management of fish populations, it has become increasingly evident that the introduction of various fish viruses into areas presently free of virus must be limited. Consequently, emphasis is currently being placed on the development of procedures to regulate the transport of fish and fish eggs at the state, national and international levels. The establishment of such procedures for the transport of fish depends, in part, upon the development of methods for the detection and isolation of fish viruses. While the applicability of various techniques such as immunofluorescence (Piper et al. 1973) for the detection of fish viruses has been demonstrated, the generally accepted procedure is based on the isolation of the virus in susceptible cell cultures (Gillespie et al. 1974).

Infectious pancreatic necrosis (IPN) virus causes a highly destructive disease of young trout. Survivors usually become lifelong carriers and continuously shed virus in ovarian fluid, sperm, and feces. The mechanisms by which a virus establishes a carrier state in survivors of an epizootic disease are not understood; thus, the detection of virus in carrier fish may present particular problems. This report describes the occurrence of interference in the isolation of IPN virus from carrier fish.

Methods — Six brook trout (*Salvelinus fontinalis*), 7–8 inches in length, and suspected of being carriers of IPN virus, were divided into two pools of three

Printed in Canada (J3680)
Imprimé au Canada (J3680)

TABLE 1. Cytopathic effect (CPE) and virus yield in RTG-2 cell cultures infected with 0.1 ml of various dilutions of tissue homogenates of brook trout (*Salvelinus fontinalis*) suspected of carrying IPN virus and incubated at 20 C for 72 h.

	Fish Pool #1				Fish Pool #2			
	Dilution				Dilution			
	10^{-1}		10^{-3}		10^{-1}		10^{-3}	
Time After Infection (h)	CPE[a]	Virus yield[b]	CPE	Virus yield	CPE	Virus yield	CPE	Virus yield
24	0	ND[c]	2+	ND	0	ND	2+	ND
48	0	ND	4+	ND	0	ND	4+	ND
72	0	3.0	4+	8.4	1+	2.7	4+	8.2

[a] 4+, complete CPE (complete destruction of the monolayer); 2+, moderate CPE; 1+, slight CPE; 0, no CPE.
[b] Log_{10} TCID_{50} per 1.0 ml.
[c] ND = Not Done.

fish each. Whole kidneys, spleens, and a portion of the livers of the fish in each pool were removed and suspended in approximately 9 vol of Hank's Balanced Salts Solution (HBSS). The tissue was then homogenized in a Waring blendor and filtered through a 0.45-nm Millipore filter. This was considered a 10^{-1} dilution of the original tissue preparation. A 10^{-3} dilution of each tissue homogenate was also made in HBSS. Three tubes containing monolayers of RTG-2 cell cultures were then inoculated with 0.1 ml of either the 10^{-1} or 10^{-3} dilutions of the tissue homogenates of each organ pool and incubated at 20 C. The infected RTG-2 cell cultures were observed daily for cytopathic effect (CPE).

Following incubation for 72 h after infection, the cells and supernatant fluids of two tubes of each group were combined and the cells ruptured by sonic vibration for 1 min at 20 kc with a Sonic Dismembrator (Quigley-Rochester, Inc.). This suspension was filtered and the yield of infectious IPN virus was determined using a microtitration technique described by Piper et al. (1973).

Results — As indicated in Table 1, at 72 h after infection, cultures of RTG-2 cells infected with a 10^{-1} dilution of tissue homogenate from both organ pools failed to show any viral cytopathic effect (CPE). However, cultures of RTG-2 cells infected with 10^{-3} dilutions of the same homogenates exhibited extensive CPE of the type characteristic for IPN virus. Moreover, these cultures showed a considerable degree of CPE as early as 24 h after infection. Continued incubation of the cells infected with the more concentrated tissue homogenate for a total of 6 days failed to demonstrate CPE.

Likewise, very little infectious IPN virus was obtained from the concentrated homogenates, but cell cultures that were infected with the more dilute suspensions resulted in virus titers of $10^{8.2}$ and $10^{8.4}$ TCID_{50} per ml. The identity of the IPN virus was confirmed by virus neutralization tests as described previously (Piper et al. 1973).

Considering the results presented above, if the more concentrated sample had been tested alone, the detection of IPN virus in these fish would most likely have failed. This report, therefore, describes an instance of interference in the isolation of IPN virus from carrier fish. The exact nature of this interference is not known.

In recent years, much attention has been focused on the study of homologous viral interference. This phenomenon involves an intracellular interference that is active only against homologous, or even homotypic viruses, and has been demonstrated in numerous systems (Huang 1973). This interference is caused by the presence of defective-interfering (DI) particles in the virus population that contain a part of the viral genome, normal structural proteins, replicate only in the presence of standard helper virus and interfere specifically with the intracellular growth of homologous standard virus (Huang 1973). The proportion of DI particles in most virus populations can be increased by continuous undiluted passage of the virus in susceptible cell cultures. When DI particles are present in virus preparations, diluted passage in susceptible cell cultures results in the production of more infectious standard virus particles than when passed undiluted. The possible role of DI particles in the establishment of chronic or carrier disease states has been suggested (Huang 1973) and recently Palma and Huang (1974) have presented evidence that the interdependence between DI and standard particles could account for viral persistence with only localized damage to the infected host. We have previously shown (Nicholson and Dunn 1974) that under some circumstances homologous viral interference does occur in trout and Atlantic salmon cell cultures infected with IPN virus and that IPN virus is, quite likely, a DI particle producing system similar to that described for other viruses. Furthermore, we have successfully established IPN-carrier cell cultures by infecting RTG-2 cells with interfering IPN virus (unpublished data).

If virus isolated from IPN carrier fish contains significant amounts of DI particles, homologous viral interference could quite likely occur and explain the results presented in this report.

It should be noted, however, that other factors could result in the failure to detect significant infectious IPN virus in cell cultures infected with relatively concentrated tissue homogenates. Possibly the tissue contained some viral inhibitor(s) that could have been eliminated by further dilution. A possible but unlikely alternative is that the tissue homogenate may have been cytotoxic and injured the cells sufficiently to interrupt virus replication but not enough to elicit any obvious deleterious effects.

Nevertheless, it is obvious that some type of interference in the replication of IPN virus can occur when relatively concentrated tissue homogenates and virus suspensions are used to infect cell cultures. It appears, therefore, that under certain circumstances, the use of 10^{-1} dilutions of tissue homogenates as cell culture inocula may fail to detect IPN virus when more diluted material may give positive results. This observation reinforces the need to include several dilutions of tissue homogenates as inocula for cell cultures when examining fish for the presence of IPN virus. A detailed investigation is needed to elucidate the mechanism of the interference observed.

Acknowledgments — This investigation was supported, in part, by a grant from the Maine Agricultural Experiment Station and the University of Maine Faculty Research Funds Committee.

GILLESPIE, D. C., T. P. T. EVELYN, C. FRANTSI, R. M. MACKELVIE, AND/ET N. NEUFELD. 1974. Methods for the detection of certain pathogens of salmonid fishes/Méthodes de détection de certains agents pathologènes chez les salmonidés. Fish. Res. Board Can. Misc. Spec. Publ. 23: 19 p./21 p.

HUANG, A. S. 1973. Defective interfering viruses. Annu. Rev. Microbiol. 27: 101–117.

NICHOLSON, B. L., AND J. DUNN. 1974. Homologous viral interference in trout and Atlantic salmon cell cultures infected with infectious pancreatic necrosis virus. J. Virol. 14: 180–182.

PALMA, E. L., AND A. HUANG. 1974. Cyclic production of vesicular stomatitis virus caused by defective interfering particles. J. Infect. Dis. 129: 402–410.

PIPER, D., B. L. NICHOLSON, AND J. DUNN. 1973. Immunofluorescent study of the replication of infectious pancreatic necrosis virus in trout and Atlantic salmon cell cultures. Infect. Immun. 8: 249–254.

Life History Observations on the Puget Sound Rockfish, *Sebastes emphaeus* (Starks, 1911)[1]

LAWRENCE L. MOULTON

Friday Harbor Laboratories and Fisheries Research Institute,
University of Washington, Seattle, Wash., 98195, USA

MOULTON, L. L. 1975. Life history observations on the Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911). J. Fish. Res. Board Can. 32: 1439–1442.

Large concentrations of Puget Sound rockfish (*Sebastes emphaeus*) were found at three locations in the San Juan Islands, Washington, at depths ranging from 10 to 25 m. Spawning females were found in August and September, the latest maturing *Sebastes* in this region. The existence of ripe females indicates that the taxon is not the juvenile form of another species. Total lengths of mature females ranged from 130 to 179 mm, and wet weights from 21 to 79 g. Fecundity estimates ranged from 20,177 for a 150-mm female to 57,103 for a 179-mm specimen. The age at maturity ranged from age II to age IV. Field and aquarium behavioral observations indicate that the species is adapted to crevice and cave existence in areas of strong currents and rocky substrate.

---

[1] Contribution No. 420, College of Fisheries, University of Washington, Seattle, Wash., U.S.A.

Printed in Canada (J3697)
Imprimé au Canada (J3697)

MOULTON, L. L. 1975. Life history observations on the Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911). J. Fish. Res. Board Can. 32: 1439–1442.

De grandes concentrations de rascasses du Puget Sound (*Sebastes emphaeus*) ont été trouvées à trois endroits dans la région des îles San Juan, Washington, à des profondeurs de 10 à 25 m. On a trouvé des femelles en fraie en août et septembre, les *Sebastes* à maturité la plus tardive de la région. La présence de femelles mûres indique que l'espèce n'est pas la forme juvénile d'une autre espèce. La longueur totale des femelles mûres varie de 130 à 179 mm, le poids humide de 21 à 79 g. La fécondité, estimée à partir de cinq femelles, varie de 20,177 chez une femelle de 150 mm à 57,103 chez un spécimen de 179 mm. L'âge de la maturité s'étale de II à IV. Des observations de comportement sur le terrain et en aquarium indiquent que l'espèce est adaptée à une existence dans les crevasses et cavernes, là où il y a forts courants et substrat rocheux.

Received January 15, 1975
Accepted April 28, 1975

Reçu le 15 janvier 1975
Accepté le 28 avril 1975

THE Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911) is a seldom reported species from the San Juan region of Puget Sound. Since the original description, nine records have been obtained from Seattle to Henry Island (Miller and Borton 1974) (Table 1). Because of its small size (maximum 179 mm), some investigators (C. Hitz, B. Miller personal communications) believed the taxon might actually be a juvenile form of another species. This occurred with the yelloweye rockfish, *Sebastes ruberrimus*, the young of which were described as *Sebastodes bilineata* by Welander and Alverson (1954) (Hart 1973).

The current study was undertaken when large concentrations of the Puget Sound rockfish were reported in the vicinity of the Friday Harbor Laboratories (FHL) in August 1973 by D. W. Gotshall. The objectives were to determine the validity of the species designation and to obtain basic life history information for the species.

Methods — Observations and most of the collecting were carried out on 61 SCUBA dives from April 1974 to March 1975, mainly at three locations — the Cantilever Pier at the Friday Harbor Laboratories, Shady Cove, and Point George, Shaw Island (Fig. 1). Collecting was done primarily by spearing, or by anesthetizing fish with a mixture of 10% quinaldine in isopropanol, which was squirted into crevices containing fish. When the fish lost equilibrium, they were netted and placed in a 20-liter carboy containing fresh sea water. Also, five individuals were caught by hook and line.

Fish were identified by keys provided in Hart (1973) and Hitz (1965) and compared with the original description in Starks (1911).

Total length to the nearest millimeter, and wet weight to the nearest gram, were measured for all fish. For females used in fecundity estimates, the ovary was removed and the fish and ovary weighed separately. Five subsamples of each ovary were removed, individually weighed, the eggs counted, and the fecundity calculated. For age determinations, otoliths were removed, cleared, and read in 50% glycerin against a black background utilizing a dissecting microscope and reflected light.

Behavioral observations were made in a 60 × 130 × 25 cm rectangular tank with 10–15 cm angular rocks, shells, and a cave structure provided as substrate material.

Observations and discussion — Many ripe females were seen at the Cantilever Pier on August 11 and 13, 1974 at a depth of 12–17 m. By August 25, the apparent proportion of spent females had increased. The few ripe females that were captured at Shady Cove on September 8 immediately released their young, and none were seen after early October. The August–September spawning period is the latest season for parturition among *Sebastes* in this region (Westrheim et al. 1968a; Westrheim et al. 1968b; Harling et al. 1971). The existence of ripe females confirms that the Puget Sound rockfish is not a juvenile form of another species.

Eight fish examined in the study exceeded the previously recorded maximum length of 16 cm (Table 2). The minimum recorded size at maturity was 130 mm. Fecundity estimates increased with size, ranging from 20,177 for a 150-mm specimen to 57,103 for a 179-mm specimen. Ripe females represented three year-classes, the youngest being age II. The oldest fish recorded was an age IV female.

Field observations from June to October revealed large populations of adult Puget Sound rockfish at three locations in the San Juan Channel: Cantilever Pier, Shady Cove, and Turn Island. The observed depth range was from 10 m to greater than 25 m. In addition, small groups of age 0 and age I fish were found at Pt. George, Shaw Island, Reid Rock, and near the Friday Harbor Laboratories dock between 12 and 17 m from June to March. Juveniles (approximately 25–30 mm) first appeared at Shady Cove and Pt. George in January and February. Gotshall (letter to A. C. DeLacy, August 1973) reported many individuals between 20 and 35 m. This contrasts with Starks' (1911) observation that the

TABLE 1. Historical record of Puget Sound rockfish (*Sebastes emphaeus*) observations.

Location	Date	Collector	Source
Griffin Bay, San Juan Is	July 22, 1932	Miller and class	UW Museum Log #2159
Friday Harbor, SJI	July 30, 1932	Chapman and DeLacy	UW Museum Log #2200
Clinton, Whidbey Is	Apr. 19, 1933	DeLacy and Chapman	UW Museum Log #2723
Elliot Bay, Seattle	May 7, 1933	DeLacy and Chapman	UW Museum Log #2727
Upright Head, Lopez Is	Apr. 15, 1968	C. Vandersluys	FHL Log Book
Cantilever Pier, FHL, SJI	Aug. 1973	D. Gotshall	D. Gotshall (letter to A. C. DeLacy)
Keystone Jetty, Whidbey Is	1973–74	D. Sommerton	D. Sommerton diving log
Edmonds Oil Dock, Edmonds	1973–74	D. Sommerton	D. Sommerton diving log
Henry Is	Nov. 30, 1974	C. Eaton	C. Eaton (personal communication)

TABLE 2. Life history information from 18 *Sebastes emphaeus* caught in 1974.

Date of capture	Age (*yr*)	Length (*mm*)	Weight (g)	Sex	Fecundity	Fecundity 95% conf. int.
June 23	1	68	—	—	—	
June 13	1	77	—	—	—	
Sept. 8	2	134	26	spent female	—	
Aug. 13	2	148	40	ripe female	20,437	18,779–22,095
Aug. 11	2	150	35	spent female	—	
Aug. 11	2	150	46	ripe female	20,177	18,936–21,418
Aug. 13	3	130	21	spent female	—	
Sept. 8	3	144	34	spent female	—	
Aug. 11	3	160	47	spent female	—	
Aug. 13	3	160	58	ripe female	24,435	21,095–27,775
Aug. 13	3	169	68	ripe female	43,984	42,734–45,234
Aug. 13	3	179	79	ripe female	57,103	54,663–59,543
Aug. 27	4	173	67	ripe female	—	
June 14	—	171	67	—	—	
May 2	—	167	50	—	—	
May 2	—	163	45	—	—	
Apr. 29	—	166	61	—	—	
Apr. 27	—	173	53	—	—	

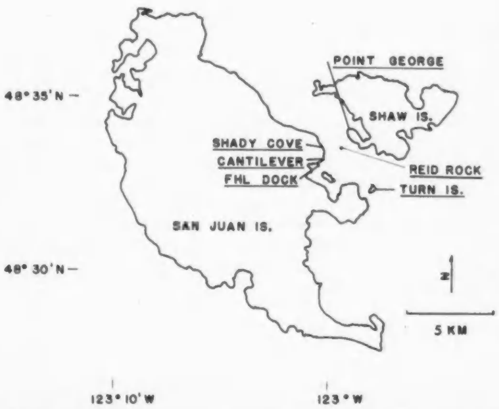


FIG. 1. Locations containing Puget Sound rockfish (*Sebastes emphaeus*).

species was most abundant in deeper waters, approximately 100 m. The discrepancy probably results from the different sampling methods used.

The adults exhibited two behavior patterns. Often, small groups (3–10 fish) would rest in contact with a rock or hover motionless inside crevices or small caves. When approached, these fish would squeeze tightly into the crevices. Others swam actively away from the rocks either individually or in loosely associated groups (individuals 1–1½ m apart). When approached, these fish would dart away, but not necessarily into shelter. In the fall, the numbers of fish present declined dramatically and most of the individuals seen by November were huddled in caves either singly or in small groups.

Fish held in an aquarium exhibited a constant behavior pattern. All would rest with the tips of the pectoral rays in contact with a solid object: the side of the tank, a rock, shell, or the cave structure provided. If an object were placed so that a pectoral fin could not touch it, the fish became restless and would search for a proper resting place. The fish stayed in close association with each other in one end of the tank. Aggression or territoriality were not evident. All fed readily on chopped shrimp or clam and were not disturbed by movements outside the tank.

All three areas with large numbers of Puget Sound rockfish exhibit similar environmental characteristics: strong currents, steep slopes, and caves and crevices formed by rock piles, boulders, or cracks in ledges. Associated species sighted on almost all dives included black rockfish (*Sebastes melanops*), yellowtail rockfish (*S. flavidus*), quillback rockfish (*S. maliger*), copper rockfish (*S. caurinus*), tiger rockfish (*S. nigrocinctus*), kelp greenling (*Hexagrammos decagrammus*), lingcod (*Ophiodon elongatus*), and longfin sculpin (*Jordania zonope*). The observed behavior of touching the tips of the pectoral fins to solid objects when selecting a resting area may be an adaptation to select small crevices which afford greater protection from predation. The apparent scarcity of the species up to this time may be an artifact of the habitat preference. The rocky areas in which the Puget Sound rockfish is found do not permit efficient operation of traditional sampling equipment.

Acknowledgments — Financial support for this project was from the Friday Harbor Laboratories' "Shaw Island Project" and from the Washington Sea Grant Project "Ecology and Distribution of Puget Sound Fishes," NOAA Grant No. 04-3-158-42. Thanks go to the many diving partners who made this study possible: B. S. Miller, C. Birkeland, R. Shimek, R. Tam, and R. Strathmann. An inquiry to B. Miller and A. C. DeLacy by D. W. Gotshall, California Fish and Game, initiated the study.

Harling, W. R., M. S. Smith, and N. A. Webb. 1971. Preliminary report on maturity, spawning season, and larvae identification of rockfishes (Scorpaenidae) collected during 1970. Fish. Res. Board Canada MS Rep. 1137: 26 p.

Hart, J. L. 1973. Pacific fishes of Canada. Bull. Fish. Res. Board Can. 80: 740 p.

Hitz, C. R. 1965. Field identification of northeastern Pacific rockfish (*Sebastodes*). U.S. Dep. Int. Fish. Wildl. Ser. Circ. 203: 59 p.

Miller, B. S., and S. F. Borton. 1974. Geographical distribution of Puget Sound fishes: maps and data source sheets. Rep. to the Wash. State Dep. Ecol., Cont. No. 74–142, Nov. 14, 1974.

Starks, E. C. 1911. Results of an ichthyological survey about the San Juan Island, Washington. Ann. Carnegie Mus. 7: 162–213.

Welander, A. D., and D. L. Alverson. 1954. New and little known fishes of the eastern Pacific. Wash. Dep. Fish. Res. Pap. 1(2): 37–44.

Westrheim, S. J., W. R. Harling, and D. Davenport. 1968a. Preliminary report on maturity, spawning season, and larvae identification of rockfishes (*Sebastodes*) collected off British Columbia in 1967. Fish. Res. Board Can. MS Rep. 951: 23 p.

Westrheim, S. J., W. R. Harling, D. Davenport, and M. S. Smith. 1968b. Preliminary report on maturity, spawning season, and larvae identification of rockfishes (*Sebastodes*) collected off British Columbia in 1968. Fish. Res. Board Can. MS Rep. 1005: 28 p.

Distribution of Hyperiid Amphipods off the Oregon Coast

H. (Van Arsdale) Lorz and W. G. Pearcy
School of Oceanography, Oregon State University, Corvallis, Oreg. 97331, USA

Lorz, H. V., and W. G. Pearcy. 1975. Distribution of hyperiid amphipods off the Oregon coast. J. Fish. Res. Board Can. 32: 1442–1447.

A total of 19 species of hyperiid amphipods was collected from 1963 to 1967 off Oregon. *Parathemisto pacifica, Paraphronima gracilis, Streetsia challengeri, Tryphana malmi, Hyperia medusarum, Hyperoche medusarum*, and *Primno macropa* were common. New distributional records are reported for *Scina crassicornis bermudensis* and *Lanceola loveni*. Abundance and occurrence of common species are lower inshore than offshore suggesting centers of abundance are in offshore-oceanic waters. Yearly changes in occurrence and abundance of hyperiid amphipods inshore may be related to coastal upwelling. There was no evidence for vertical migrations or diel differences at depth intervals of 0–150 m and 150–450 m.

Printed in Canada (J3616)
Imprimé au Canada (J3616)

LORZ, H. V., AND W. G. PEARCY. 1975. Distribution of hyperiid amphipods off the Oregon coast. J. Fish. Res. Board Can. 32: 1442–1447.

Un total de 19 espèces d'amphipodes hypériens furent recueillis de 1963 à 1967 au large de l'Orégon. *Parathemosto pacifica, Paraphronima gracilis, Streetsia challengeri, Tryphana malmi, Hyper medusarum, Hyperoche medusarum* et *Primno macropa* étaient communs. Nous signalons des extensions d'aire pour *Scina crassicornis bermudensis* et *Lanceola loveni*. Les espèces communes sont moins abondantes et se rencontrent moins fréquemment près du rivage qu'au large, ce qui suggère que les centres d'abondance se trouvent dans les eaux du large et océaniques. Les changements annuels d'occurrence et d'abondance des hypériens du littoral peuvent être liés aux remontées d'eaux profondes près de la côte. Il n'y a pas d'indications de migrations verticales ou de différences nycthémérales dans les intervalles de profondeur de 0–150 m et 150–450 m.

Received November 12, 1974 Reçu le 12 novembre 1974
Accepted March 13, 1975 Accepté le 13 mars 1975

AMPHIPODS of the suborder Hyperiidea are often important components of pelagic communities and sometimes rank third in abundance of the marine crustacean zooplankters. Moreover, hyperiid amphipods are an important food source for oceanic fishes (Iversen 1962; LeBrasseur 1966).

Distributions of hyperiid amphipod in the northeast Pacific have been reported by Thorsteinson (1941), Bowman (1953, 1960, 1973), Brusca (1967), and Sanger (1972, 1973). The purpose of this study was to describe the abundance, distribution, and seasonal occurrence of hyperiid amphipods off Newport, Oregon from June 1963 to June 1967.

Materials and methods — Collections were taken with 1-m diameter plankton nets (0.571-mm mesh) from June 1963 to June 1967 at stations 15 and 25 nautical miles offshore (inshore stations) and 50–65 nautical miles offshore (offshore stations) along the 44°39′N parallel. Prior to January 1964, 18 oblique tows were made with a net 8–9 m long, towed 4–6 knots, descending at 50 m/min and ascending at 30 m/min. After January 1964 all tows were vertical, using a net 4 m long, descending at 50 m/min and ascending at 30 m/min. All oblique and vertical collections were taken at night to a depth of about 200 m (depth permitting). A total of 144 collections was made. In addition, 68 collections were made 50 nautical miles offshore to study vertical and diel variations. Opening–closing 1-m nets were actuated by pressure-activated wire cutters (Yentsch et al. 1962). The nets were towed obliquely, in tandem, and sampled the approximate depth intervals of 0–150 m and 150–450 m. A TSK flow-meter in the mouth of nets provided estimates of the volumes of water filtered.

Samples were preserved in 10% formalin aboard ship. In the laboratory, hyperiid amphipods were sorted from the whole sample if they numbered less than 200. If they were more numerous, the whole sample was divided by a plankton splitter until about 200 hyperiids remained.

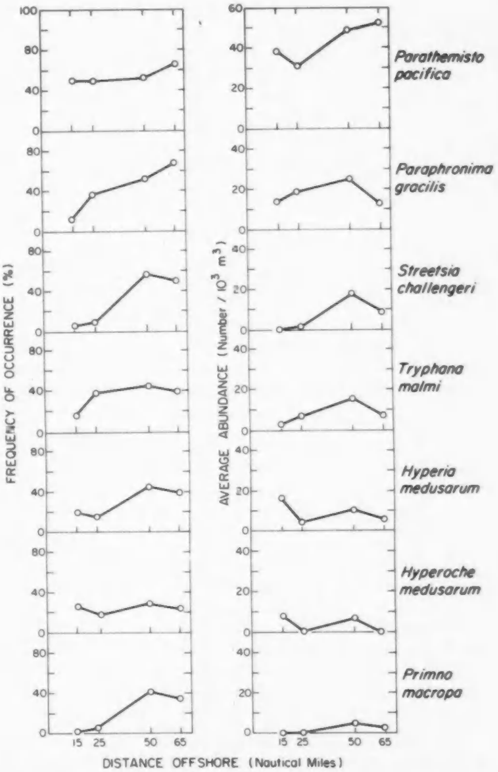


FIG. 1. Frequency of occurrence and average abundance of common species at four stations off Newport, Oreg., June 1963–June 1967.

Species composition — A total of 19 species of hyperiid amphipods was collected off Oregon (Table 1). To our knowledge *Lanceola loveni* has not been reported from the eastern North Pacific and *Scina crassicornis bermudensis* has not been reported from the North Pacific. According to T. E. Bowman (personal communication), who

TABLE 1. Total numbers and frequency of occurrence of hyperiid amphipods collected off Newport, June 1963–67.

	Total number	Frequency of occurrence
Parathemisto pacifica Stebbing 1888	6279	0.56
Paraphronima gracilis Claus 1879	2930	0.42
Streetsia challengeri Stebbing 1888	1227	0.36
Tryphana malmi Boeck 1870	1122	0.35
Hyperia medusarum (Müller 1776)	1367	0.31
Hyperoche medusarum (Krøyer 1838)	1353	0.24
Primno macropa Guérin 1836	626	0.22
Phronima sedentaria (Forskal 1775)	174	0.18
Vibilia armata Bovallius 1887	669	0.10
Lycaea pulex Marion 1874	65	0.06
Oxycephalus clausi Bovallius 1887	102	0.06
Primno sp.	44	0.04
Paraphronima crassipes Claus 1879	34	0.03
Dairella californica (Bovallius 1885)	60	0.03
Vibilia wolterecki Behning 1939	36	0.03
Vibilia propinqua Stebbing 1888	9	0.02
Cystisoma fabricii Stebbing 1888	5	0.02
Lanceola loveni Bovallius 1885	3	0.01
Scina crassicornis bermudensis Shoemaker 1945	1	0.01

identified our specimen of *S. crassicornis bermudensis* Shoemaker, this species is distinct from *Scina curlensis* Vinogradov, which has been previously reported from the North Pacific. Van Arsdale (1967) reported new distributional records from *Streetsia challengeri*, *Cystisoma fabricii*, *Lycaea pulex*, and *Tryphana malmi*. Sanger (1973) extended the northern ranges of *T. malmi* and *S. challengeri* to 54°N and *L. pulex* to 50°N.

The following six common species will be discussed further: *Parathemisto pacifica*, *Paraphronima gracilis*, *Streetsia challengeri*, *Tryphana malmi*, *Hyperia medusarum*, *Hyperoche medusarum*, and *Primno macropa*.

Parathemisto pacifica — This is the most common species in the eastern North Pacific (Bowman 1960; Sanger 1973). Off Oregon it was highest in total number and frequency of occurrence (Table 1). Average abundance and frequency of occurrence were highest offshore (Fig. 1). *Parathemisto pacifica* occurred during all seasons of most years with highest catches in the summer, except inshore in 1963 and 1966 (Table 2). This species was more abundant and frequent in 0–150 m than 150–450 m collections at 50 nautical miles (Table 3). Though average abundance was higher in the upper 150 m during night than day, this difference was not significant (*t*-test, $P > 0.05$).

Paraphronima gracilis — This species was second in total abundance and frequency of occurrence (Table 1). Frequency of occurrence increased with distance from shore but average abundance increased to 50 nautical miles and then decreased (Fig. 1). Bowman (1953) found *P. gracilis* to be abundant and widespread nearshore. Seasonally, abundance was lowest inshore in summer; offshore abundance did not fluctuate greatly (Table 2). The average abundance and frequency of occurrence of *P. gracilis* was higher in 0–150 m than 150–450 m (Table 3). No significant diel differences were found in either depth interval. Thus, there was no evidence for vertical migration of this species off Oregon. Brusca (1967), however, reported that this species migrates vertically off California.

Streetsia challengeri — Frequency of occurrence and average abundance of *S. challengeri* increased to 50 nautical miles and then decreased (Fig. 1). It was not common inshore. Abundance offshore was greatest during the winter for all years except 1965 (Table 2). This species was more abundant and frequent from 0–150 m than from 150–450 m (Table 3). Day–night differences within these strata were not significant, hence, there was no evidence of vertical migration. Brusca (1967), however, felt there was evidence of diurnal migration toward the surface at night.

Table 2. The average abundance per 1000 m^3 of common species from inshore and offshore stations off Newport, Oreg. during four seasons from June 1963 to June 1967. Blank spaces indicate no samples were taken.

	1963		1964		1965		1966		1967	
	Inshore	Offshore	Inshore	Offshore	Inshore	Offshore	Inshore	Offshore	Inshore	Offshore
Parathemisto pacifica										
Spring			26	47	20	4	124	45	37	27
Summer	0	168	42	66	81	49	10	59		
Fall	95	15	37	35	4	12	27	8		
Winter	16	70	22	63	55	0	91	39	90	97
Paraphronima gracilis										
Spring			75	8	4	12	0	15	0	8
Summer	0	98	0	8	3	10	9	12		
Fall	0	54	26	7	68	15	39	6		
Winter	26	45	14	15	15	7	23	15	2	12
Streetsia challengeri										
Spring			0	0	0	5	0	9	2	18
Summer	5	36	0	2	5	10	0	3		
Fall	4	18	0	0	0	8	8	12		
Winter	<1	203	0	15	2	0	11	14	3	21
Tryphana malmi										
Spring			17	4	2	0	0	0	8	7
Summer	0	3	0	0	14	6	6	5		
Fall	8	21	10	19	5	7	8	7		
Winter	11	48	0	25	4	14	14	11	5	21
Hyperia medusarum										
Spring			0	7	<1	6	0	2	9	3
Summer	0	6	0	0	2	5	18	15		
Fall	35	14	0	7	0	2	3	10		
Winter	3	33	0	5	0	14	184	16	30	16
Hyperoche medusarum										
Spring			0	13	1	0	0	0	4	5
Summer	0	0	0	0	2	5	3	3		
Fall	492	0	0	6	3	4	12	8		
Winter	20	198	7	0	0	2	12	9		
Primno macropa										
Spring			0	7	0	3	0	4	0	5
Summer	0	0	0	14	14	11	10	0		
Fall	0	0	0	0	0	8	2	3		
Winter	0	2	0	6	0	0	0	3	1	1

Tryphana malmi — Frequency of occurrence and average abundance of this fourth most common species increased with distance from shore to 50 nautical miles (Fig. 1). Highest abundance occurred offshore in fall and winter with the exception of 1965 (Table 2). Highest abundance and frequency of occurrence were in the 0–150 m interval (Table 3). No evidence was found for diel differences or vertical migration.

Hyperia medusarum — This species, a synonym of *Hyperia hystrix*, is the most common species of *Hyperia* along the Pacific coast of North America (Bowman 1973). It was fifth in total number and frequency of occurrence off Oregon (Table 1). The frequency of occurrence was greater offshore while average abundance was highest at 15 nautical miles (Fig. 1). Abundance was greatest in fall or winter months (Table 2). Day–night differences were not significant within or between depths. Frequency of occurrence was highest from 150 to 450 m (Table 3).

Hyperoche medusarum — Ranking sixth in total abundance, this species was highest in frequency of occurrence and abundance at 15 and 50 nautical miles (Fig. 1). Generally, greatest seasonal abundance occurred during fall and winter months (Table 2). Day–night differences gave no evidence of vertical migration (Table 3).

Primno macropa — This species was rare inshore and increased offshore in both frequency of occurrence and average abundance (Fig. 1). Larg-

TABLE 3. Vertical and diel differences, means ($\bar{x}$), and frequency of occurrence (f.o.) of 68 collections taken 50 nautical miles off Newport.

	0–150 m		150–450 m	
	Day	Night	Day	Night
Parathemisto pacifica				
$\bar{x}$	9.64	51.12	2.80	2.50
f.o.	0.63	0.94	0.46	0.50
Paraphronima gracilis				
$\bar{x}$	11.50	28.11	2.50	3.08
f.o.	0.68	0.94	0.60	0.41
Streetsia challengeri				
$\bar{x}$	12.73	13.94	2.40	0.67
f.o.	0.54	0.70	0.33	0.16
Tryphana malmi				
$\bar{x}$	5.41	3.24	0.80	1.50
f.o.	0.54	0.64	0.26	0.41
Hyperia medusarum				
$\bar{x}$	3.86	1.88	2.73	2.92
f.o.	0.31	0.29	0.80	0.50
Hyperoche medusarum				
$\bar{x}$	1.54	1.14	0.05	0.13
f.o.	0.22	0.17	0.07	0.08
Primno macropa				
$\bar{x}$	3.40	0.88	9.20	7.33
f.o.	0.31	0.17	0.80	0.75

est catches were generally made during the summer months (Table 2). There was no evidence of vertical migration; abundance and frequency of occurrence were highest from 150 to 450 m (Table 3).

Discussion — The lower abundance and frequency of occurrence inshore than offshore (Fig. 1, Table 2) indicate that most of the species of hyperiids off Oregon have centers of abundance in offshore-oceanic waters. Numbers inshore may be affected by seasonal changes in advection. During upwelling periods, when winds are from the north and surface waters are displaced offshore, the catches inshore were usually low. With the change in the wind regime during November through February from a northerly to a southerly direction, there is a net onshore movement of surface water (Burt and Wyatt 1964). During this period the occurrence and abundance of hyperiids were usually at a maximum inshore (Van Arsdale 1967; present data for 1965–67). Also, hyperiid amphipods were usually more abundant during warm years than during cool years, especially at the inshore stations (Van Arsdale 1967). Advection of surface water, therefore, may be related to both seasonal and year-to-year changes in the inshore occurrence of hyperiid amphipods.

Acknowledgments — Dr T. E. Bowman of the Smithsonian Institution gave valuable assistance in recommendation of literature and confirmation of species identifications. This research was supported by the National Science Foundation (Grant GB-1588) and the Office of Naval Research (Contract N000-14-67-A-0369-0007 under project NR083-102).

BOWMAN, T. E. 1953. The systematics and distribution of pelagic amphipods of the families Vibiliidae, Paraphronimidae, Hyperiidae, Dairellidae, and Phrosinidae from the Northeastern Pacific. Ph.D. Thesis. Univ. California, Los Angeles, Calif. 430 p.

1960. The pelagic amphipod genus *Parathemisto* (Hyperiidea: Hyperiidae) in the North Pacific and adjacent Arctic Ocean. Proc. U.S. Nat. Mus. 112(3439): 343–392.

1973. Pelagic amphipods of the genus *Hyperia* and closely related genera (Hyperiidea: Hyperiidae). Smithson. Contrib. Zool. 136: 1–76.

BRUSCA, G. J. 1967. The ecology of pelagic amphipods I: Species accounts, vertical zonation and migration of amphipods from the waters off southern California. Pac. Sci. 21: 382–393.

BURT, W. V. and B. WYATT. 1964. Drift bottle observations of the Davidson Current off Oregon, p. 156–165. *In* K. Yoshida [ed.] Studies on oceanography. Univ. of Washington Press, Seattle, Wash.

IVERSEN, R. T. B. 1962. Food of Albacore tuna, *Thunnus germo* (Lacpede) in the central and northeastern Pacific. U.S. Fish Wildl. Serv. Fish. Bull. 214: 495–479.

LeBrasseur. R. J. 1966. Stomach contents of salmon and steelhead trout in the northeastern Pacific Ocean. J. Fish. Res. Board Can. 23: 85–100.

Sanger, G. A. 1972. Pelagic amphipod crustaceans from the southeastern Bering Sea. NWFC MARMAP Survey I. Rep. No. I. 24 p. (Nat. Mar. Fish. Ser., N.W. Fish. Center, Seattle, Wash.).

1973. Epipelagic amphipods (Crustacea) off Washington and British Columbia, October–November 1971. NWFC MARMAP Survey I. Rep. No. 8. 29 p. (Nat. Mar. Fish. Ser., N.W. Fish. Center, Seattle, Wash.).

Thorsteinson, E. D. 1941. New or noteworthy amphipods from the North Pacific coast. Univ. Wash. Publ. Oceanogr. 4: 50–94.

Van Arsdale, H. A. 1967. The distribution of hyperiid amphipods off the Oregon coast. M.S. Thesis. Oregon State Univ. Library, Corvallis, Oreg. 34 p.

Yentsch, C. S., G. D. Grice, and A. Hart. 1962. Some opening–closing devices for plankton nets operated by pressure, electrical, and mechanical actions. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 153: 59–65.

Young Witch Flounder, *Glyptocephalus cynoglossus*, on the Slope off Virginia[1]

Douglas F. Markle

Virginia Institute of Marine Science, Gloucester Pt., Va. 23062, USA

Markle, D. F. 1975. Young witch flounder, *Glyptocephalus cynoglossus*, on the slope off Virginia. J. Fish. Res. Board Can. 32: 1447–1450.

Young witch flounder, *Glyptocephalus cynoglossus*, 11–25 cm TL, are abundant on the continental slope off Virginia. The Virginian slope may be a major nursery area for 1- to 3- or 4-yr-old witch flounder spawned by one or more northern stocks. Shelf water circulation patterns are considered as a possible mechanism for the passive dispersal of larvae.

Markle, D. F. 1975. Young witch flounder, *Glyptocephalus cynoglossus*, on the slope off Virginia. J. Fish. Res. Board Can.32: 1447–1450.

Il y a abondance de jeunes plies grises, *Glyptocephalus cynoglossus*, de 11 à 25 cm de LT sur la pente continentale du large de la Virginie. Il se peut que la pente virginienne soit une région d'alevinage pour les plies grises de 1à 3 ou 4 ans issues de stocks septentrionaux. La circulation des eaux de pente est peut-être le mécanisme responsable de la dispersion passive des larves.

Received February 10, 1975
Accepted April 25, 1975

Reçu le 10 février 1975
Accepté le 25 avril 1975

In the western North Atlantic, witch flounder, *Glyptocephalus cynoglossus*, have been caught from off Cape Lookout, North Carolina (34°09.4′N 75°44.5′W, unpublished Virginia Institute of Marine Science trawl records) to the Strait of Belle Isle (Bigelow and Schroeder 1953; Powles and Kohler 1970). In the northern part of the range, juveniles less than 30 cm TL are found at depths of 144–450 m (Powles and Kohler 1970), but on the continental slope off Virginia juveniles are a dominant species around 900 m (Markle and Musick 1974). Witch flounder are found in depths of 18–1565 m (Bigelow and Schroeder 1953), an unusually broad depth range first noticed by Goode and Bean (1896), but not adequately understood until Powles and Kohler (1970) showed that juveniles lived deeper than adults. This note documents the abundance of witch flounder by size, depth, and temperature on the continental slope off Virginia and presents new information on its complex life history.

Methods — The data are a by-product of an intensive trawling program in Norfolk Canyon, between latitudes 36°58′N and 37°10′N, and an area of the open slope, between 36°34′N and 36°46′N, at depths of 75–2000 m. Additional trawling was conducted between Chesapeake Bay and Norfolk Canyon in depths of 20–70 m. Two cruises were made on R/V *Iselin* (June 4–16, 1973) and R/V *Gilliss* (November

---

[1] Virginia Institute of Marine Science Contribution No. 684.

Printed in Canada (J3724)
Imprimé au Canada (J3724)

13–25, 1974). Thirty-minute tows were made with a semi-balloon otter trawl with a 45-ft (13.7 m) headrope and a 0.5-inch (12.7 mm) stretched mesh codend liner. Total (TL) or standard lengths (SL) were recorded for each fish, with SL converted to TL for this report. Fish over 80 mm SL were estimated using: $TL = -17.9 + 1.31$ (millimeters SL) and those under 80 mm were estimated using: $TL = SL + 0.1$ (millimeters SL).

Results — During the two cruises, witch flounder were caught at every station deeper than 256 m and shallower than 1080 m (44 stations, 2161 individuals, Fig. 1). The shoalest capture was at 166 m in June and the deepest at 1408 m in November. Witch flounder were caught at bottom salinities of 34.9–35.7% and temperatures of 4.1–11.3 C.

Between June and November samples there was no significant difference in mean TL ($t = 1.36603$), mean depth ($t = 1.34770$), or mean bottom temperature ($t = 1.51357$) of the stations at which witch flounder were captured. Witch flounder were occupying the same range of depth and temperature in both months.

However, when depth and bottom temperature of capture were weighted by the number of individuals captured, there were significant differences. Witch flounder were caught in significantly ($t = 22.2366^{***}$) deeper water in November ($\overline{X} = 670$ m) than in June ($\overline{X} = 492$ m) and in significantly ($t = 27.69444^{***}$) cooler water in November ($\overline{X} = 5.5$ C) than in June ($\overline{X} = 7.3$ C). Since occasional samples contained very large numbers of witch flounder (Fig. 1), the number caught at each temperature and depth were transformed by $y = \ln x$ (Taylor 1953). The results showed that witch flounder were still caught significantly ($t = 3.02203^{**}$) deeper in November ($\overline{X} = 650$ m) than in June ($\overline{X} = 527$ m) and in significantly ($t = 3.79181^{***}$) cooler water in November ($\overline{X} = 5.8$ C) than in June ($\overline{X} = 7.1$ C). Thus, although witch flounder occurred over the same depth and temperature ranges, a significant number of individuals had moved 125–175 m deeper from June to November.

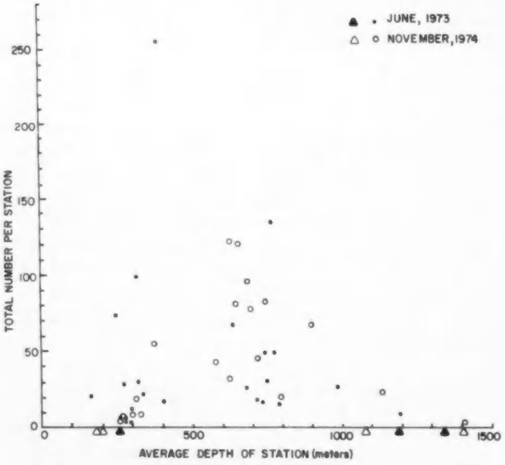


FIG. 1. Depth distribution of witch flounder (*Glyptocephalus cynoglossus*) on the slope off Virginia during June 1973 and November 1974. Stations within the depth range 166–1408 m that captured no witch flounder are represented by triangles.

About 90% of the catch was between 10 and 24 cm TL in June (Fig. 2B) and between 14 and 26 cm TL in November (Fig. 2C). A collection of juveniles from Nova Scotia (Fig. 2A) (Powles and Kohler 1970) had a greater number of larger individuals with about 90% of the catch between 12 and 33 cm TL. The mean TL was significantly greater ($t = 2.76894^{**}$) in November (19.1 cm) than in June (18.7 cm), but the mode in June is greater than in November (Fig. 2). This appears to be due to rapid growth and/or recruitment of smaller fish and a precipitous decline in numbers of larger fish from June to November.

The slope of the linear regression of mean TL on depth of a station was not significantly different from zero in either month, nor was the slope of mean TL on bottom temperature in June significant. In November the regression, $\overline{TL} = 125.8 + 14.0$ (T°C), was significant ($F_{(1,17)} = 7.56^{*}$). The upper and lower 95% confidence limits on the slope were 24.8 and 3.3, respectively. Half of the specimens over 30 cm TL in November were caught at one station around 300 m and 9.6 C, the third highest temperature recorded in November. This sample no doubt affected the significance of the regression.

Discussion — In June there was an indication of length frequency modes around 10, 14, 18, and 21 cm (Fig. 2B). The first mode probably represents age-class I since the pelagic larval stage may last as long as 6 mo (Bigelow and Schroeder 1953) and the first year's growth is variously reported as 6–8 cm (Powles and Kennedy 1967) or 8–10 cm (Bowers 1960). The other modes represent either 2- and 3-yr-old fish by Bowers' (1960) estimates, or 2-, 3- and 4-yr-old fish by Powles and Kennedy's (1967) data. In November the length frequency distribution changed and the modes were very indistinct. The relatively narrow size range observed in the collections off Virginia and the strongly bimodal length frequency distribution from the Nova Scotia Banks

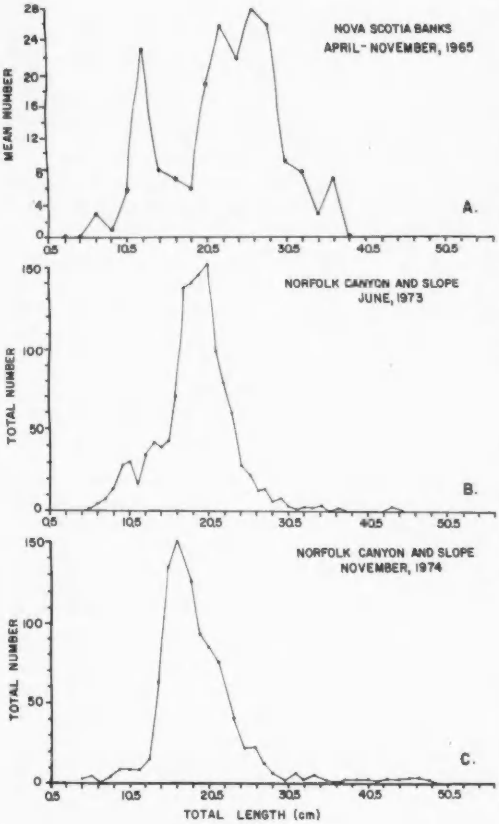


FIG. 2. Length-frequency distribution for young witch flounder from: A, Nova Scotia Banks, April–November, 1965, from Powles and Kohler 1970, figure 4; B, Norfolk Canyon and slope off Virginia, June 1973; and C, Norfolk Canyon and slope off Virginia, November 1974.

(Fig. 2) invites the inference that the slope off Virginia serves as a nursery for 1-, to 3- or 4-yr-old witch flounder. However the source of these fish might be implied, it is at present unknown.

In the Gulf of Maine, including the offshore banks, eggs of witch flounder have been captured from April (Colton and St. Onge 1974) to August (Bigelow and Schroeder 1953) and pelagic larvae from May (Colton and St.Onge 1974) to early November (Bigelow and Schroeder 1953). Bigelow and Schroeder (1953) believed that that area had the most southerly spawning stocks of witch flounder, since there was no evidence of significant spawning west of Cape Cod. However, during seasonal trawling on the continental shelf off Virginia adults up to 50 cm TL were frequently captured during the winter of 1967–68 (J. A. Musick personal communication). During the present study, a few adults up to 48 cm TL were also captured in November. These larger individuals may represent strays, part of a southward winter migration of northern stocks, or even a southern breeding stock. At present the only indication of spawning off Virginia is nine larvae, 6–15 mm TL, caught over the continental shelf in May 1960 (Massmann et al. 1961). The statement that no significant spawing occurs west of Cape Cod (Bigelow and Schroeder 1953) cannot be refuted at present. However, larger larvae have been caught over the shelf off Virginia in June, August, and October 1966 (Clark et al. 1969), and several recently metamorphosed postlarvae, 4–10 cm TL, were captured in both months of this study.

If significant spawning occurs only north of Georges Bank, then witch flounder off Virginia probably originate from one or more northern stocks. This raises several questions. It is possible that the populations off Virginia are stunted expatriates that contribute nothing to northern stocks. An analysis of the age and growth of Virginian witch flounder, although beyond the scope of this study, would be interesting. Alternatively, the occurrence of juvenile concentrations off Virginia, in areas that are not commercially fished, may act as an important, additional conservation mechanism (Powles and Kohler 1970) against overfishing of the species.

An additional question concerns the mechanism whereby larvae or demersal juveniles get to the slope off Virginia. Since witch flounder off Virginia occupy about the same temperature range as those in the Gulf of Maine and Gulf of St. Lawrence (0–10 C, Bigelow and Schroeder 1953), the early demersal juveniles may simply travel southward along the increasingly deeper isotherms. Another plausible mechanism is provided by shelf water circulation patterns. Surface shelf water circulation patterns are probably most important for larval dispersal since larvae are found over the shelf and above the thermocline (Powles and Kohler 1970).

A westerly flow from Georges Bank and Great South Channel extends south of Long Island (Bumpus and Lauzier 1965), and off the Middle Atlantic States this becomes a broad southerly flow with a significant onshore component. A marked offshore component from Chesapeake Bay to Cape Hatteras (Bumpus and Lauzier 1965; Norcross and Stanley 1967) turns the flow eastward where it becomes entrained between the Gulf Stream and slope water in the upper

200 m of the water column (Ford et al. 1952). This summary of circulation is simplified and ignores such variation as the surface reversal of flow off the Middle Atlantic States during some summers (Norcross and Stanley 1967). However, it does provide a general outline of a passive transport system for a long-lived larva. Thus, it could account for the presence of recently metamorphosed witch flounder off Virginia, as well as contribute to an explanation of the southern limit of the species.

Acknowledgments — I am grateful to Drs J. V. Merriner and J. A. Musick for reviewing the manuscript; to my wife for preparing the figures; and to both referees for comments that improved the manuscript. This research was supported by N.S.F. Grant No. GA-37561, J. A. Musick, principal investigator.

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. U.S. Fish Wildl. Serv. Fish. Bull. 74: 577 p.

BOWERS, A. B. 1960. Growth of the witch (*Glyptocephalus cynoglossus* (L.) in the Irish Sea. J. Cons. Cons. Int. Explor. Mer 25: 168–176.

BUMPUS, D. F. 1960. Sources of water contributed to the Bay of Fundy surface circulation. J. Fish. Res. Board Can. 17: 181–197.

1973. A description of the circulation on the continental shelf of the east coast of the United States. Prog. Oceanogr. 6: 111–157.

BUMPUS, D. F., AND L. M. LAUZIER. 1965. Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Am. Geogr. Soc. Serial Atlas of the Marine Environment. Folio 7. 4 p.

CLARK, J., W. G. SMITH, A. W. KENDALL JR., AND M. P. FAHAY. 1969. Studies of estuarine dependence of Atlantic coastal fishes. U.S. Fish Wildl. Serv., Bur. Sport Fish. Wildl. Tech. Pap. 28: 132 p.

COLTON, J. B. JR., AND J. M. ST.ONGE. 1974. Distribution of fish eggs and larvae in continental shelf waters, Nova Scotia to Long Island. Am. Geogr. Soc., Serial Atlas of the Marine Environment. Folio 23. 2 p.

FORD, W. L., J. R. LONGARD, AND R. E. BANKS. 1952. On the nature, occurrence and origin of cold low salinity water along the edge of the Gulf Stream. J. Mar. Res. 11: 281–293.

GOODE, G. B., AND T. H. BEAN. 1896. Oceanic ichthyology. U.S. Nat. Mus. Spec. Bull. 553 p.

MARKLE, D. F., AND J. A. MUSICK. 1974. Benthic slope fishes found at 900 m depth along a transect in the western N. Atlantic Ocean. Mar. Biol. 26: 225–233.

MASSMANN, W. H., J. J. NORCROSS, AND E. B. JOSEPH. 1961. Fishes and fish larvae collected from Atlantic plankton cruises of R/V *Pathfinder*, December 1959 – December 1960. Va. Inst. Mar. Sci. Spec. Sci. Rep. 26: 1–15.

NORCROSS, J. J., AND E. M. STANLEY. 1967. Inferred surface and bottom drift, June 1963, through October 1964. *In* Circulation of shelf waters off the Chesapeake Bight. Prof. Pap. ESSA 3(2): 11–42.

POWLES, P. M., AND V. S. KENNEDY. 1967. Age determination of Nova Scotian greysole, *Glyptocephalus cynoglossus* L., from otoliths. Int. Comm. Northwest Atl. Fish. Res. Bull. 4: 91–100.

POWLES, P. M., AND A. C. KOHLER. 1970. Depth distribution of various stages of witch flounder (*Glyptocephalus cynoglossus*) off Nova Scotia and in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 27: 2053–2062.

TAYLOR, C. C. 1953. Nature of variability in trawl catches. U.S. Fish Wildl. Serv. Fish. Bull. 54(83): 145–166.

Preheat Treatment for Improvement of Frozen Storage Stability at —10 C in Fillets and Minced Flesh of Silver Hake (*Merluccius bilinearis*)

BARBARA SMITH LALL, ALISON R. MANZER, AND DORIS FRASER HILTZ

Department of the Environment, Fisheries and Marine Service,
Halifax Laboratory, Halifax, N.S. B3J 2R3

LALL, B. S., A. R. MANZER, AND D. F. HILTZ. 1975. Preheat treatment for improvement of frozen storage stability at –10 C in fillets and minced flesh of silver hake (*Merluccius bilinearis*). J. Fish. Res. Board Can. 32: 1450–1454.

Dimethylamine (DMA) formation occurs in the muscle of silver hake (*Merluccius bilinearis*) during frozen storage. The rate of its formation in fillets and minced flesh during subsequent frozen storage for 1 mo at –10 C is not affected by preheating at temperatures up to 60 C. Preheating to 80 C, however, greatly retards DMA development. Lipid hydrolysis (free fatty acid accumulation) is arrested by preheating to 60 C, but is little affected by preheating at temperatures up to 45 C. These deteriorative reactions are faster in minced flesh than in fillets, and in materials prepared from summer (spawning) fish than in those prepared from winter fish.

Printed in Canada (J3699)
Imprimé au Canada (J3699)

In breaded fishery products, preheat treatment as presently practiced is insufficient to inactivate these deteriorative enzymic reactions in sensitive gadoid species such as the hakes and pollocks.

LALL, B. S., A. R. MANZER, AND D. F. HILTZ. 1975. Preheat treatment for improvement of frozen storage stability at −10 C in fillets and minced flesh of silver hake (*Merluccius bilinearis*). J. Fish. Res. Board Can. 32: 1450–1454.

Il se forme de la diméthylamine (DMA) dans le muscle du merlu argenté (*Merluccius bilinearis*) durant l'entreposage réfrigéré. Sa vitesse de formation dans les filets et la chair hachée au cours d'un entreposage réfrigéré subséquent d'un mois à −10 C n'est pas affectée par un préchauffage à des températures allant jusqu'à 60 C. Par contre, un préchauffage à 80 C retarde beaucoup la formation de DMA. L'hydrolyse des lipides (accumulation d'acides gras libres) est arrêtée par un préchauffage à 60 C, mais est peu affectée par un préchauffage à des températures allant jusqu'à 45 C. Ces altérations se produisent plus rapidement dans la chair hachée que dans les filets, et dans des produits préparés à partir de poissons d'été (en fraie) que dans ceux provenant de poissons d'hiver.

Pour ce qui est des produits pannés, le préchauffage tel que présentement pratiqué ne suffit pas à inactiver ces réactions enzymatiques altérantes chez des espèces de gadoïdes aussi sensibles que les merlus, merluches et goberges.

Received January 20, 1975
Accepted April 23, 1975

Reçu le 20 janvier 1975
Accepté le 23 avril 1975

THE formation of dimethylamine (DMA) and formaldehyde (FA) in the muscle by enzymatic degradation of trimethylamine oxide (TMAO) is a major change during frozen storage of gadoid fish (Castell et al. 1971; Tokunaga 1974). The sensitivity of these species to frozen storage deterioration is in large part due to complexing of the FA with protein, which results in increasing loss of protein solubility and in textural toughening (Dyer 1973; Castell et al. 1973; Tokunaga 1974). These deteriorative reactions, as with many enzymatic changes associated with loss in quality of frozen fish (Dyer 1968), are particularly rapid at temperatures in the −5 to −10 C range, with decreasing activity at lower temperatures (Castell et al. 1970; Dyer 1973; Tokunaga 1974).

Utilization of gadoid species in the form of "precooked," convenience-type fishery products has increased dramatically in recent years, but the degradative changes in these products during subsequent frozen storage have been little studied. Precooking was found to inhibit lipid hydrolysis in frozen fillets of herring (Bosund and Ganrot 1969) and of cod presteamed for 90 min (Olley and Lovern 1960), and to retard rancidity development in frozen fillets of both herring and cod (Bosund and Ganrot 1970). It also reduced sharply, but did not eliminate, the production of DMA in some frozen gadoid species (Castell et al. 1971); however, heating for 5 min at 100 C was sufficient to destroy the DMA-forming activity induced by an extract from pyloric caeca of Alaska pollock, an active source of the enzyme (Yamada and Amano 1965), although the cofactor required for activity was found to be heat-stable (Yamada et al. 1969).

In preliminary work we found that DMA is formed in the muscle of silver hake (*Merluccius bilinearis*) during frozen storage. This note concerns the effect of preheating muscle of this species to various temperatures on its subsequent stability in frozen storage. Both intact fillets and minced flesh were studied. Minced flesh has large potential for use in processed fish products, but in the primary form (as frozen minced blocks) it may be more unstable than intact flesh; this is true for Pacific hake (Babbitt et al. 1972), and for cod and Atlantic pollock if gadoid kidney tissue is present (Dingle and Hines 1975).

Materials and methods — In the first experiment, frozen samples prepared from silver hake caught at sea (Emerald Basin) in March 1974, and held 2 days on the vessel in refrigerated sea water at 0–1 C before processing, were used. Intact skinless fillets, and minced flesh prepared by passing headed, gutted fish through a Bibun deboner with a drum having 5-mm diameter holes, were packaged immediately in approximately 100 g lots in polyethylene bags, quick-frozen in a plate freezer at −40 C, and stored in wax-coated cardboard cartons for 12 wk at −26 C before use. Under these storage conditions, differences between initial (prefreezing) and poststorage values in the properties tested were negligible.

In the second experiment, unfrozen samples of minced flesh (prepared as above) from inshore silver hake taken in mackerel traps in June 1974 were used; the round fish were held overnight in ice before processing. These fish were larger (38–45 cm) than the off-shore hake (25–33 cm), were sexually mature, and had been feeding actively, their stomachs being gorged with mackerel. To minimize possible deteriorative changes in the raw material, the minced flesh was chilled immediately after processing and used for heat treatment within 2 h.

For preheating, samples of uniform size, about 5 cm long by 5 cm wide by 2.5 cm thick (about 80 g), tightly enclosed in polyethylene bags, were immersed in water baths maintained at 3–5 C higher than the desired internal temperature of the samples (0–80 C). To monitor internal temperature change, copper–constantan thermocouples connected to a recording potentiometer were inserted in the geometric center of two additional samples included with the experimental samples in each bath. When the desired temperature had been reached (within 30–60 min, or 2.5 h in the case of the frozen samples brought to 0 C), the experimental samples were immediately cooled rapidly to −10 C either in a plate freezer or by immersion in an ethylene glycol bath at −15– −20 C. They were then placed in wax-coated cardboard boxes for storage in a constant-temperature cabinet at −10 ± 0.2 C; this temperature is high enough for the enzymic reactions to proceed at a reasonable rate, and moreover, may frequently be reached in commercial practice, especially within the distribution and marketing chain (e.g. Lentz and Foley 1968). Control samples (unheated) brought rapidly to −10 from −26 C (first experiment) or from 0 C (second experiment) were also stored.

Deteriorative reactions during storage at −10 C were monitored at frequent intervals by measurement of dimethylamine nitrogen (DMA-N) (Dyer and Mounsey 1945), extractable protein nitrogen (EPN) (Dyer et al. 1964), and free fatty acid (FFA) (Bligh and Scott 1966).

Results — Preheating of frozen samples of silver hake from −26 C to either 0, 35, or 60 C had little or no effect on the rate of DMA formation during subsequent frozen storage at −10 C in either intact fillets or in minced flesh (Fig. 1). In all cases, the rates were similar to those in the control (unheated) samples, at least up to 25–30 days storage. Upon continued storage, there may have been a trend toward lower DMA production in preheated fillet samples compared with control fillets. The decrease in EPN, which occurred concomitantly with DMA production, proceeded at about the same rate in the samples prewarmed to 0 C as in control samples. In samples preheated to 35 and 60 C, heat-denaturation rendered the bulk of the protein immediately inextractable in neutral salt solution. Figure 1 also shows that the deteriorative reactions of DMA formation and EPN loss during frozen storage were considerably faster in minced flesh than in intact fillets, confirming results of a previous study on silver hake in this laboratory (Hiltz et al. 1974).

On the other hand, lipid hydrolysis as measured by increase in FFA content was arrested in both fillets and minced flesh preheated to 60 C (Fig. 2), presumably as a result of thermal inactivation of the lipolytic enzymes. However, the rate of FFA formation was little affected by prewarming to 0 or 35 C.

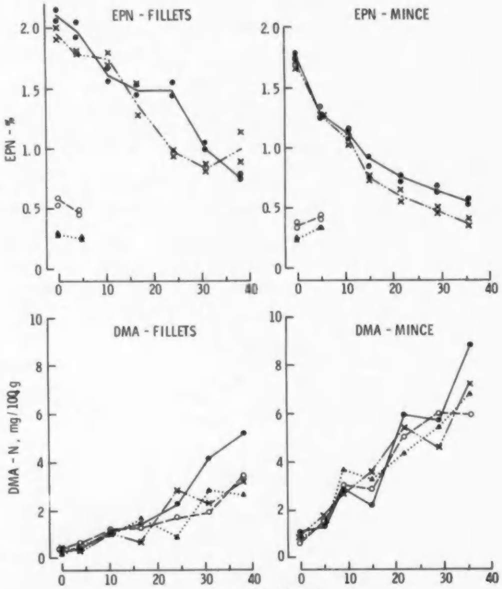


FIG. 1. Extractable protein nitrogen (EPN) and dimethylamine (DMA) changes during frozen storage at −10 C in samples of fillets and minced flesh of winter-caught silver hake preheated from −26 C to 0, 35, and 60 C, and immediately cooled to −10 C. ●——●, control (unheated); ×—·—×, preheated to 0 C; ○- - -○, preheated to 35 C; ▲.......▲, preheated to 60 C.

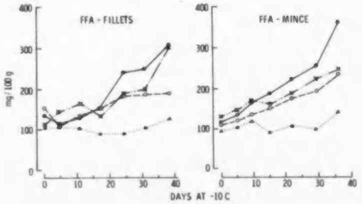


FIG. 2. Accompanying changes in content of free fatty acids (FFA) during storage at −10 C of the preheated samples of silver hake given in Fig. 1. Symbols as in Fig. 1.

These results were confirmed and extended in a second experiment using unfrozen samples of minced flesh of inshore, summer-caught silver hake (Fig. 3). Preheating at temperatures up to 60 C again did not influence the initial rate of DMA formation, which was very rapid in this material at −10 C, although this treatment tended to slow subsequent DMA production. Preheating to 80 C, however, was found to retard DMA

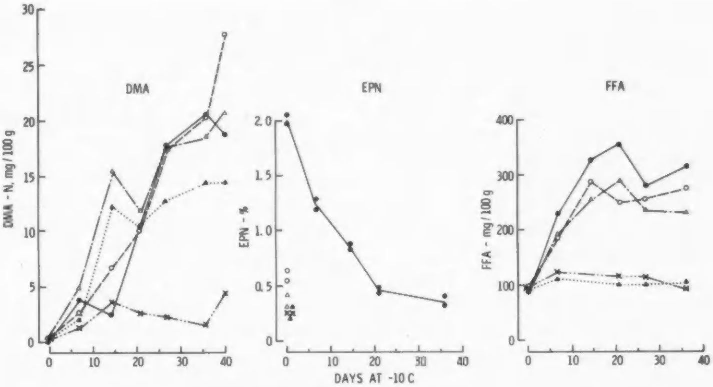


Fig. 3. Changes in dimethylamine, extractable protein nitrogen, and free fatty acids during frozen storage at −10 C of samples of fresh (unfrozen) minced flesh of summer-caught silver hake preheated to 35, 45, 60, and 80 C, and immediately cooled to −10 C. ●——●, control (unheated); ○- - -○, preheated to 35 C; △—·—△, preheated to 45 C; ▲........▲, preheated to 60 C; ×———×, preheated to 80 C.

formation drastically. Lipid hydrolysis was inhibited in samples preheated to 60 C, as found in the previous experiment, and to 80 C, but not in samples brought to 35 or 45, although the rate of FFA accumulation in these may have been slowed slightly. The rapid decrease in EPN of the control samples was coincident with the rate of DMA formation.

Discussion — The flesh of the gadoid silver hake has the capability to form DMA rapidly in frozen storage at −10 C, although the rate of its development in fillets prepared from winter-caught fish was not as fast as that found in comparable fillets of red hake (*Urophycis chuss*) at this temperature (Dyer and Hiltz 1974). (The data of Castell et al. (1971), attributed erroneously to silver hake [*Merluccius bilinearis*], actually referred to red hake, *Urophycis chuss*.) Minced flesh of silver hake was much more sensitive to the deteriorative reactions than intact fillets. The DMA formation was about twice as rapid in minced flesh prepared from large, spawning, summer-caught fish as in comparable material from smaller, winter-caught fish (compare control curve for minced flesh in Fig. 1 with control curve in Fig. 3); these differences may be due to seasonal variations, as suggested by Castell et al. (1971).

It is apparent that the DMA-forming mechanism in gadoid muscle, presumably enzyme-catalyzed (Yamada and Amano 1965), is quite heat-resistant; we found that preheating fillets and minced flesh of silver hake to temperatures up to 60 C had little or no effect on the rate of DMA formation during subsequent frozen storage for 1 mo at −10 C (samples were at 55–60 C for 10–12 min before cooling began). Only in samples preheated to 80 C was the activity severely reduced, though not eliminated. Castell et al. (1971) also encountered thermostability of the DMA-producing mechanism in gadoid flesh, in that precooking (steaming 5 min followed by autoclaving 10 min at 110 C) did not inhibit, but only slowed, DMA formation during subsequent storage at −5 C. Tokunaga (1964), on the other hand, reported that preheating Alaska pollock muscle (30-g samples) for 30 min in a 50 C bath arrested DMA production during subsequent frozen storage at −17 C. It is likely that the longer heating time for these small samples at the lower temperature (50 C) was sufficient to inactivate the enzyme, although species variation in enzyme properties may be involved.

The heat stability of the DMA-forming mechanism and, to a lesser extent, of the lipid hydrolytic activity, indicates that, under present processing conditions, many types of secondary products utilizing gadoid fish species will be subject to extensive deterioration under poor frozen storage conditions. In current practice, fish sticks and other breaded products are frequently prepared from frozen blocks of fillets or minced flesh, and in their preparation, the temperature of the fish portion rarely exceeds 0–5 C during the frying of the breaded material. In products where temperatures as high as 35 C may be reached, the protein is heat-denatured and hence FA would cause little further deterioration, but the continuing production of DMA in frozen storage may impair flavor of the product.

The present work suggests that the frozen storage stability of processed fishery products from "susceptible" gadoids like the hake species, cusk and pollock could be markedly improved if the fish flesh were sufficiently precooked to inactivate enzymic mechanisms. The temperature and time of cooking required, however, need definition.

Acknowledgments — We are grateful to Dr W. J. Dyer for his encouragement and for helpful discussions.

The winter fish were obtained as part of a collaborative project with the Department of Fisheries, Province of Nova Scotia. We thank D. W. Lemon of this laboratory for handling and care of the fish on the vessel.

BABBITT, J. K., D. L. CRAWFORD, AND D. K. LAW. 1972. Decomposition of trimethylamine oxide and changes in protein extractability during frozen storage of minced and intact hake (*Merluccius productus*) muscle. Agr. Food Chem. 20: 1052–1054.

BLIGH, E. G., AND M. A. SCOTT. 1966. Lipids of cod muscle and the effect of frozen storage. J. Fish. Res. Board Can. 23: 1025–1036.

BOSUND, I., AND B. GANROT. 1969. Effect of pre-cooking of Baltic herring on lipid hydrolysis during subsequent cold storage. Lebensm. Wiss. Technol. 2: 59–61.

1970. Effect of pre-cooking on lipid oxidation and storage life of frozen fish. Lebensm. Wiss. Technol. 3: 71–73.

CASTELL, C. H., W. NEAL, AND B. SMITH. 1970. Formation of dimethylamine in stored frozen sea fish. J. Fish. Res. Board Can. 27: 1685–1690.

CASTELL, C. H., B. SMITH, AND W. J. DYER. 1973. Effect of formaldehyde on salt extractable proteins of gadoid muscle. J. Fish. Res. Board Can. 30: 1205–1213.

CASTELL, C. H., B. SMITH, AND W. NEAL. 1971. Production of dimethylamine in muscle of several species of gadoid fish during frozen storage, especially in relation to presence of dark muscle. J. Fish. Res. Board Can. 28: 1–5.

DINGLE, J. R., AND J. A. HINES. 1975. Protein instability in minced flesh from fillets and frames of several commercial Atlantic fishes during storage at –5 C, particularly in the presence of gadoid kidney tissue. J. Fish. Res. Board Can. 32: 775–783.

DYER, W. J. 1968. Deterioration and storage life of frozen fish, p. 429–447. *In* J. Hawthorne [ed.] Low temperature biology of foodstuffs. Pergamon Press, Inc., New York, N.Y.

1973. New technical research on frozen fish. Refrigeration 48: 38–41. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 2656, 1973)

DYER, W. J., H. BROCKERHOFF, R. J. HOYLE, AND D. I. FRASER. 1964. Polyphosphate treatment of frozen cod. I. Protein extractability and lipid hydrolysis. J. Fish. Res. Board Can. 21: 101–106.

DYER, W. J., AND D. F. HILTZ. 1974. Sensitivity of hake muscle to frozen storage. Fish. Res. Board Can. Halifax Technol. Res. Lab. New Ser. Circ. 45: 5 p.

DYER, W. J., AND Y. A. MOUNSEY. 1945. Amines in fish muscle. II. Development of trimethylamine and other amines. J. Fish. Res. Board Can. 6: 359–367.

HILTZ, D. F., W. J. DYER, AND D. W. LEMON. 1974. Some properties of fillets and minced flesh of silver hake (*Merluccius bilinearis*) in frozen storage. Fish. Res. Board Can. Halifax Technol. Res. Lab. New Ser. Circ. 46: 9 p.

LENTZ, C. P., AND M. A. FOLEY. 1968. Survey of temperatures in frozen fish shipped by road. Can. Inst. Food Technol. J. 1: 123–125.

OLLEY, J., AND J. A. LOVERN. 1960. Phospholipid hydrolysis in cod flesh stored at various temperatures. J. Sci. Food Agric. 11: 644–652.

TOKUNAGA, T. 1964. Studies on the development of dimethylamine and formaldehyde in Alaska pollock muscle during frozen storage. I. Rep. Hokkaido Reg. Fish. Res. Inst. 29: 108–122. (Transl. from Japanese by Torry Transl. No. 745, 1972)

1974. The effect of decomposed products of trimethylamine oxide on quality of frozen Alaska pollock fillet. Bull. Jap. Soc. Sci. Fish. 40: 167–174. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3117, 1974)

YAMADA, K., AND K. AMANO. 1965. Studies on the biological formation of formaldehyde and dimethylamine in fish and shellfish. V. On the enzymatic formation in the pyloric caeca of Alaska pollock. Bull. Jap. Soc. Sci. Fish. 31: 60–64.

YAMADA, K., K. HARADA, AND K. AMANO. 1969. Biological formation of formaldehyde and dimethylamine in fish and shellfish. VIII. Requirement of cofactor in the enzyme system. Bull. Jap. Soc. Sci. Fish. 35: 227–231.

Comparative Toxicity of Larval Lampricide (TFM: 3-trifluoromethyl-4-nitrophenol) to Selected Benthic Macroinvertebrates[1]

ALAN W. MAKI,[2] LESTER GEISSEL, AND HOWARD E. JOHNSON

Department of Fisheries and Wildlife, Michigan State University, East Lansing, Mich. 48824, USA

MAKI, A. W., L. GEISSEL, AND H. E. JOHNSON. 1975. Comparative toxicity of larval lampricide (TFM: 3-trifluoromethyl-4-nitrophenol) to selected benthic macroinvertebrates. J. Fish. Res. Board Can. 32: 1455–1459.

The acute toxicity of larval lampricide (TFM: 3-trifluoromethyl-4-nitrophenol) to 35 species of benthic macroinvertebrates was determined in 96-h flow-through tests. The 96-h LC50 values range from 2.1 mg/liter for blackfly larvae, *Simulium pugetense*, to values in excess of 38.0 mg/liter for species with heavy exoskeletons: crayfish (*Orconectes propinquus*), dobsonfly larvae (*Chauloides* sp), and dragonfly naiads (*Ophiogomphus* sp.) Younger individuals of the clam (*Ligumia* sp.) and the mayfly nymph (*Ephemerella cornuta*) were 2 to 1.5 times more sensitive than larger individuals of the same species. Early emergence of adults and increased locomotor activity were observed among some organisms exposed to sublethal concentrations.

MAKI, A. W., L. GEISSEL, AND H. E. JOHNSON. 1975. Comparative toxicity of larval lampricide (TFM: 3-trifluoromethyl-4-nitrophenol) to selected benthic macroinvertebrates. J. Fish. Res. Board Can. 32: 1455–1459.

Nous avons mesuré la toxicité aiguë du lampricide larvaire (TFM: 3-trifluorométhyl-4-nitrophénol) sur 35 espèces de macroinvertébrés benthiques lors d'essais de 96 h dans un débit d'eau continu. Les valeurs de la CL-50 après 96 h s'étalent de 2.1 mg/litre pour les larves de simulies, *Simulium pugetense*, à plus de 38.0 mg/litre pour les espèces à exosquelette épais: *Orconectes propinquus*, larves de corydale, nymphes de *Chauloides* sp. et de libellules, *Ophiogomphus sp*. Les jeunes coques (*Ligumia* sp.) et la nymphe d'éphémère (*Ephemerella cornuta*) sont de 2 à 1.5 fois plus sensibles que les individus plus grands des mêmes espèces. Nous avons observé un émergement hâtif et une activité locomotrice accrue chez quelques organismes exposés à des concentrations sublétales.

Received November 8, 1974
Accepted April 7, 1975

Reçu le 8 novembre 1974
Accepté le 7 avril 1975

THE lampricide TFM (3-trifluoromethyl-4-nitrophenol) has been used extensively in Great Lakes tributaries since preliminary field tests demonstrated a selective toxicity to larval sea lampreys *Petromyzon marinus* (Applegate et al. 1961). Occasional significant mortalities of benthic macroinvertebrates have occurred following field applications of TFM (U.S Bureau of Commercial Fisheries 1960) and field studies of benthic macroinvertebrates have demonstrated significant population decreases within several taxa soon after lampricide treatment (Torblaa 1968; Haas 1970).

Static toxicity tests (Smith 1967) showed that 10 mg/liter TFM was lethal to 100% of the hydra, turbellarians, and blackfly larvae, 99% of the burrowing mayflies, 89% of the leeches, and 50% of the clams. In similar static tests, Marking (1971) determined the 96-h LC50 with a snail (*Physa* sp.) and with scuds (*Gammarus* sp.) to be 1.29 mg/liter and 1.80 mg/liter respectively. However, definitive toxicity data, citing LC-50s and associated confidence limits are unavailable for representatives from most macroinvertebrate orders.

We employed two proportional diluters to determine the toxicity of field grade TFM (36% active) to 35 benthic macroinvertebrates during continuous-flow 96-h tests.

Materials and methods — The toxicity tests were conducted at the Michigan Department of Natural Resources fish hatchery in Mecosta Co., Paris, Mich. Cheney Creek, a small spring fed stream, was the water source used in all tests. The characteristics of Cheney Creek water are summarized in Table 1.

---

[1] Michigan Agricultural Experiment Station Journal Article No. 7041.

[2] Present address: Environmental Water Quality Research Department, Procter and Gamble Company, Ivorydale Technical Center, Cincinnati, Ohio 45217, USA.

Printed in Canada (J3615)
Imprimé au Canada (J3615)

TABLE 1. Mean physical and chemical characteristics of dilution water (Cheney Creek) used in toxicity tests.

	Mean	(Range)
Alkalinity (mg/liter $CaCO_3$)	179	(176–182)
Calcium (mg/liter $CaCO_3$)	152	(144–160)
Carbon, Total (mg/liter C)	39	(38– 42)
Chloride (mg/liter Cl)	2.8	(2.2–4.0)
Specific conductance (μmho at 25 C)	397	(360–430)
Dissolved oxygen (mg/liter)	9.7	(9.2–10.1)
Hardness (mg/liter $CaCO_3$)	211	(204–214)
Iron (mg/liter Fe)	0.2	(0.1–0.2)
Nitrate (mg/liter N)	1.31	(1.05–1.57)
Nitrite (μg/liter N)	4.3	(4.0–5.0)
pH	7.79	(7.45–8.0)
Phosphorus, total (mg/liter P)	0.01	(0.01)
Sodium (mg/liter Na)	2.4	(2.0–3.0)
Solids, total (mg/liter)	231	(226–240)
Sulfate (mg/liter SO_4)	15.0	(14.0–16.0)
Temperature (C)	12.0	(11.0–13.5)

The test chambers were paired concrete hatchery channels each 3.96 × 0.61 m, and filled with 10.2 cm of water. The chambers were large enough to test several species simultaneously in each toxicant concentration. Larger species, such as crayfish and molluscs, ranged freely within the channels, and smaller species were held in 10 × 10 × 20 cm chambers construction of 0.5-mm mesh Nitex screen over a plexiglass frame.

A pair of proportional diluters provided constant toxicant concentrations in each of four test channels. Constant flow rates through each diluter system were maintained by two separate head boxes. The toxicant was metered into each diluter with a syringe pump and a 50-cm^3 syringe. The field grade TFM contained 36% active ingredient and a specific gravity of 1.212. All toxicity values were based on the percent active TFM in the formulation.

The test organisms were collected throughout the year from nearby streams. Each group of test organisms was held in a concrete channel for a minimum of 4 days before testing. Four species were exposed simultaneously, and depending upon availability, between 15 and 50 individuals of each species were exposed in each concentration. Initial toxicity tests were performed to establish the ranges of toxicity; definitive tests provided more precise estimates of the LC50 values.

Before a test, flow rates in the diluter were adjusted to 1.0 liter/min for a total replacement time of about 3.5 h based on a channel volume of 225 liters. Toxicant concentrations were kept constant by precise adjustments of the speed of the syringe pump. TFM concentrations in each chamber were monitored 4 times daily by the colorimetric method of Howell and Marquette (1962). Flow rates were relatively constant, and variations in toxicant concentration were generally less than 5%. The test organisms were considered to be dead when no movement could be detected following manual probing with a glass pipette. We placed affected individuals of several species in the control channel of flowing stream water and found the method to be a valid indicator of mortality.

The LC50 values and 95% confidence limits were calculated according to the method of Litchfield and Wilcoxon (1949). Sprague's (1969) terminology is used, and the LC50 values represent a graphic interpolation from four partial-effect concentrations.

Results and discussion — The 96-h LC50 values ranged from 2.1 mg/liter with blackfly larvae (*Simulium pugetense*) to values exceeding the maximum test concentration of 38.0 mg/liter with crayfish (*Orconectes propinquus*), dobsonfly larvae (*Chauloides* sp.), and dragonfly naiads (*Ophiogomphus* sp.) (Table 2). Among the most susceptible species to TFM were the freshwater annelid worms of the family Lumbricidae (96-h LC50 of 5.3 mg/liter) and pelecypod molluscs (96-h LC50 of 9.7 mg/liter). Susceptibility differed in size-classes of clams (*Ligumia* sp.). In comparable exposures the 96-h LC50 was 8.3 mg/liter with individuals up to 9.0 cm total length and 11.7 mg/liter for individuals greater than 15 cm total length.

A similar size-related susceptibility was observed with the mayfly nymph (*Ephemerella cornuta*). Individuals of the last instar (8 mm total length) were relatively resistant (96-h LC50, 45.6 mg/liter); early instar stages (less than 4 mm total length) were more sensitive (96-h LC50, 24.0 mg/liter. This size-related response to toxicants by invertebrates has also been observed by Sanders and Cope (1968).

An increased resistance to TFM by invertebrates with heavy exoskeletons was reported from

TABLE 2. Toxicity of Field Grade TFM (calculated as active ingredient) to macroinvertebrates. Unless specified, all insect nymphs and larvae are late instars.

Species	LC50 and 95% confidence intervals (mg/liter)	
	24 h	96 h
Pelecypoda		
Sphaerium sp. 10–15 mm	17.5 (16.84–18.21)	7.6 (6.44–8.97)
Pisidium sp. 10–12 mm	16.9 (14.93–19.13)	11.2 (10.18–12.32)
Ligumia sp. >16.0 cm	>18.0	11.7 (10.64–12.87)
Ligumia sp. <9.0 cm	>11.2	8.3 (7.03–9.79)
Isopoda		
Asellus militaris 8–10 mm	17.0 (14.41–20.06)	9.7 (8.09–11.64)
Amphipoda		
Gammarus pseudolimnaeus 10–12 mm	38.0 (32.76–44.08)	13.5 (11.74–15.53)
Decapoda		
Orconectes propinquus 3–4 mm	>36.4	>36.4
Ephemeroptera		
Hexagenia bilineata	7.9 (6.93–9.01)	3.4 (3.03–3.81)
Stenonema frontale	24.91 (22.23–27.89)	12.4 (10.42–14.76)
Stenonema luteum	29.6 (27.92–31.37)	18.3 (15.25–21.96)
Baetisca obesa	37.8 (33.16–43.09)	29.2 (27.17–33.87)
Paraleptophlebia sp.	>34.6	32.4 (27.78–39.20)
Tricorythodes sp.	29.3 (25.86–33.19)	27.0 (23.50–31.03)
Ephemerella cornuta 8 mm	>39.0	45.6 (39.53–52.62)
Ephemerella cornuta <4 mm	36.2 (31.75–41.27)	24.0 (18.46–31.20)
Baetis sp.	6.9 (6.39–7.45)	4.4 (3.79–5.10)
Isonychia bicolor	18.3 (15.77–21.23)	12.3 (10.88–13.90)
Coeon sp.	11.1 (8.88–13.87)	7.2 (5.90–8.78)
Odonata		
Ophiogomphus sp.	>38.0	>38.0
Plecoptera		
Paragnetina media	21.5 (17.92–25.81)	12.5 (10.42–15.00)
Isoperla slossonae	16.7 (13.47–20.71)	8.0 (6.72–9.52)
Acroneuria lycorias	>34.0	>34.0
Pteronarcys dorsata	32.2 (23.85–43.47)	27.1 (19.64–37.40)

TABLE 2 (*Concluded*)

Species	LC50 and 95% confidence intervals (mg/liter)	
	24 h	96 h
Megaloptera		
Cauliodes sp.	>36.0	>36.0
Trichoptera		
Brachycentrus americanus	10.5 (8.40–13.13)	6.6 (5.59–7.79)
Lepidostoma sp.	15.0 (13.64–16.50)	9.1 (8.05–10.28)
Chimarra obscura	3.8 (3.59–4.04)	2.8 (2.63–3.18)
Cheumatopsyche sp.	28.3 (24.71–32.40)	26.7 (22.25–32.04)
Hydropsyche sp.	>32.0	25.2 (15.75–40.32)
Limnephilus consocius	>39.0	>39.0
Macronemum sp.	>38.0	>38.0
Diptera		
Simulium pugetense	6.1 (5.65–6.59)	2.1 (1.78–2.48)
Pedicia sp.		>11.7
Chrysops carbonarius		>35.8
Annelida		
Lumbricidae 6–9 mm	6.6 (6.11–7.13)	5.3 (4.65–6.04)

studies in Germany (Great Lakes Biological Laboratory 1963). A similar trend was observed in the comparative LC50 values calculated in the present investigation. No mortality was observed for those test species with relatively rigid exoskeletons, e.g. crayfish, dragonfly, and hellgrammite larvae, at concentrations 5–6 times the concentration required to kill 50% of the annelid worms during a similar 96-h exposure.

Sublethal effects of TFM exposure were observed in several test species. Insect larvae exposed to TFM during the late instar stages frequently emerged as adults sooner than the controls. Also, the lampricide caused increased locomotion, e.g. hyperactivity of the arthropods and increased slime trails of pelecypod molluscs. These sublethal effects may have ecological significance in natural populations during actual stream treatment by increasing downstream drift and susceptibility to predation.

We used the methods of Howell and Marquette (1962) to conduct toxicity tests with larval lamprey (*Ichthyomyzon unicuspis*) and rainbow trout (*Salmo gairdneri*) to determine the TFM concentration that would be required for 100% effective lamprey control in Cheney Creek. The data indicated that a maximum allowable concentration for water of this particular hardness and pH (Table 1) would be 9.0 mg/liter TFM for a duration of 10–12 h during an actual lamprey control program. The toxic effects of TFM are greatly influenced by water quality; the compound being most toxic in soft acid waters. Considering the wide range of hardness and pH that may be encountered in Great Lakes tributaries, concentrations ranging from 1 to 17 mg/liter have been shown necessary for lamprey control (Dykstra and Lennon 1966).

Considering the continuous flow toxicity data, a 9.0 mg/liter treatment could be expected to cause significant mortality in six of the test species. Among the mayflies, *Hexagenia bilineata*, *Baetis* sp., and *Cloen* sp. would be expected to suffer high mortalities. The highly sensitive caddisfly, *Chimarra obscura*, may approach complete elimination in treated stream sections based on a 24-h LC50 of 3.81 mg/liter TFM. The other highly susceptible species examined during these tests, larval blackflies (*Simulium pugetense*), and aquatic earthworms (Lumbricidae), could be reduced to less than 50% of their pretreatment abundance. TFM effects on remaining test species would be expected to be minimal since the 24-h LC50 values range from 1.5 to 4 times the determined stream treatment concentration of 9.0 mg/liter.

The macroinvertebrates in this study include representative species found in typical Great Lakes tributaries of good water quality, but they represent only a small portion of the total stream fauna. Our data indicate significant mortalities in six species exposed to 9.0 mg/liter; however, 96-h exposures do not preclude the existence of long-term genetic changes, effects upon early life stages, or effects on reproduction. Indeed, the significantly greater toxicity of lampricide to younger life stages of mayflies and pelecypod molluscs indicate that a 96-h LC50 value does not ensure continued protection of a species throughout the entire life cycle.

Acknowledgments — This research was supported by Research Contract No. 14-16-0008-651 from the Bureau of Sport Fisheries and Wildlife and by the Michigan State University Agricultural Experiment Station.

APPLEGATE, V. C., J. H. HOWELL, J. W. MOFFETT, B. G. H. JOHNSON, AND M. A. SMITH. 1961. Use of TFM as a selective lamprey larvicide. Great Lakes Fish. Comm. Tech. Rep. 1: 35 p.

DYKSTRA, W. W., AND R. E. LENNON. 1966. The role of chemicals for the control of vertebrate pests, p. 29–34. *In* E. F. Knipling [Chairman] Pest control by chemical, biological, genetic, and physical means. A. Symposium. U.S. Dep. Agric., Agric. Res. Serv. 33–110.

GREAT LAKES BIOLOGICAL LABORATORY. 1963. Sea lamprey control and research program and progress, 1961, Appendix IV, p. 1–42. *In* Great Lakes Fish. Comm., Rep. Annu. Meet. June 26–27, 1963. Ann Arbor, Michigan.

HAAS R. C. 1970. The effects of lamprey larvicide on the bottom fauna and periphyton of the Chocolay River, Marquette Co., Michigan. Mich. Dep. Nat. Res., Res. Dev. Rep. 200: 1–66.

HOWELL, J. H., AND W. M. MARQUETTE. 1962. Use of mobile bioassay equipment in the chemical control of sea lamprey. U.S. Fish. Wildl. Serv., Spec. Sci. Rep. — Fish. 418: 1–9.

LITCHFIELD, J. T., AND F. WILCOXON. 1949. A simplified method of evaluating dose-effect experiments. J. Pharmacol. Exp. Ther. 97: 99–113.

MARKING, L. L. 1971. Toxicity of TFM to aquatic invertebrates, p. 28–30. *In* Progress report for 1971 in registration-oriented research on TFM used in control of the sea lamprey. Fish. Cont. Lab., LaCrosse, Wis.

SANDERS, H., AND O. B. COPE. 1968. The relative toxicities of several pesticides in naiads of three species of stoneflies. Limnol. Oceanogr. 13: 112–117.

SMITH, A. J. 1967. The effect of the lamprey larvicide, 3-trifluoromethyl-4-nitrophenol, on selected aquatic invertebrates. Trans. Am. Fish. Soc. 96: 410–413.

SPRAGUE, J. B. 1969. Measurement of pollutant toxicity to fish. I. Bioassay methods for acute toxicity. Water Res. 3: 793–821.

TORBLAA, R. L. 1968. Effects of lamprey larvicides on invertebrates in streams. U.S. Fish Wildl. Serv., Spec. Sci. Rep. — Fish. 572: 1–13.

U.S. BUREAU OF COMMERCIAL FISHERIES. 1960. Lamprey control and research in the United States, p. 37–47. *In*: Great Lakes Fish. Comm. Annu. Rep. 1960.

Hepatic Morphology and Acid Phosphatase Localization in the Channel Catfish (*Ictalurus punctatus*)

M. W. KENDALL

Department of Anatomy, School of Medicine, University of Mississippi, Jackson, Miss. 39216, USA

AND W. E. HAWKINS

Section of Microscopy, Gulf Coast Research Laboratory, Ocean Springs, Miss. 39564, USA

KENDALL, M. W., AND W. E. HAWKINS. 1975. Hepatic morphology and acid phosphatase localization in the channel catfish (*Ictalurus punctatus*). J. Fish. Res. Board Can. 32: 1459–1464.

Livers of 50 channel catfish (25–45 cm long) obtained by seining from the Ross Barnett Reservoir near Jackson, Mississippi were subjected to light, electron microscopic, and enzyme histochemical examination to describe the hepatic parenchyma and exocrine pancreas as well as localize acid phosphatase. Similar to that of other fish species, catfish liver parenchyma consisted of laminae of dual-plated muralium and, unlike that of many species, dispersed exocrine pancrea-

Printed in Canada (J3477)
Imprimé au Canada (J3477)

tic tissue was observed circumscribing the portal vein, its tributaries, hepatic artery, and its branches. Acid phosphatase activity was histochemically localized to reaction product in lysosomal-like bodies arranged in peribiliary canalicular patterns. Electron microscopic observations were consistent with the above observations and biliary canaliculi were noted with long microvillar processes occupying their lumens. The exocrine pancreatic cells contained granular endoplasmic reticulum, free ribosomes, Golgi bodies, and numerous membrane-bound zymogen granules.

Kendall, M. W., and W. E. Hawkins. 1975. Hepatic morphology and acid phosphatase localization in the channel catfish (*Ictalurus punctatus*). J. Fish. Res. Board Can. 32: 1459–1464.

Nous avons étudié en microscopie photonique et électronique et par examen histochimique des enzymes les foies de 50 barbues de rivière (25–45 cm de longueur) capturées à la senne dans le réservoir Ross Barnett, près de Jackson, Mississippi, en vue de décrire le parenchyme hépatique et le pancréas exocrine, et aussi de localiser l'acide phosphatase. Ressemblant à celui d'autres espèces de poisson, le parenchyme hépatique de la barbue de rivière est constitué de lamelles de muralium à doubles plaques et, contrairement à plusieurs espèces, on a constaté que le tissu pancréatique exocrine dispersé entoure la veine porte, ses tributaries, l'artère hépatique et ses branches. L'activité de l'acide phosphatase, déterminée histochimiquement, se trouve dans le produit de réaction, dans des corps à apparence de lysosomes disposés en réseaux de canalicules péribiliaires. Les observations au microscope électronique confirment celles décrites plus haut, et les canalicules biliaires apparaissent munis de longs procès microvillaires occupant les lumens. Les cellules pancréatiques exocrines renferment un réticulum endoplasmisque granulaire, des ribosomes libres, des corps de Golgi et de nombreux granules de zymogène enveloppés d'une membrane.

Received June 26, 1974
Accepted April 25, 1975

Reçu le 26 juin 1974
Accepté le 25 avril 1975

In this study, channel catfish (*Ictalurus punctatus*) liver morphology has been described and compared to other fish species according to liver structure and type of pancreas. The structure of the liver of vertebrates including certain fishes (carp, goldfish, and bowfin) has been investigated by Elias and Bengelsdorf (1952) and found to consist of solid masses of hepatocytes perforated by cylindrical lacunae that contained sinusoids. Also, the histochemical detection of acid phosphatase was employed to localize this enzyme inside hepatocytes, since this has proven to be a valuable method for demonstrating lysosomal changes in response to organic mercurial poisoning (Taylor 1965; Verity and Reith 1967). Since the livers of fishes are major sites of detoxification (Hogan and Knowles 1968), hepatomas (Scarpelli 1967), bacterial diseases (Bullock et al. 1971), parasitic infestations (Olsen 1967), and nutritional deficiencies (Judd and Cross 1966), the following description should be useful as a basis for comparison to affected hepatic tissue.

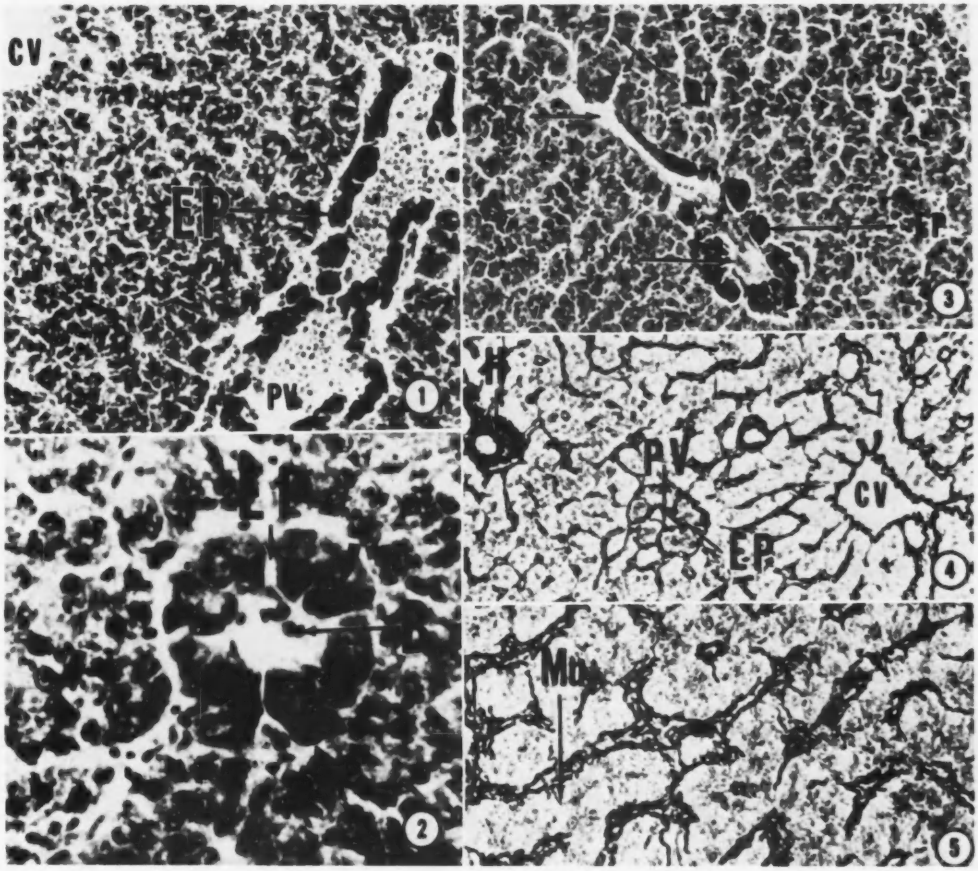
Materials and methods — Fifty channel catfish (25–45 cm long), apparently healthy and vigorous, were captured in February, 1973, by seining from the Ross Barnett Reservoir near Jackson, Mississippi.

The fish were decapitated and dissected rapidly to excise livers that were placed in cold Lavdowsky's fixative or Regaud's fixative (Lillie 1965). Tissues were subsequently transferred to 70% alcohol for storage, then dehydrated in alcohol, cleared in xylene, and embedded in paraffin. Serial sections were subsequently cut at 7μm on a rotary microtome. The staining methods employed included hematoxylin and eosin (H and E), periodic acid-Schiff's reagent plus hematoxylin (PASH) using methods of McManus and Mowry (1960), and a reticular stain technique developed by Williams (1960).

The section-freeze substitution technique of Chang and Hori (1961) was used to prepare liver tissue for acid phosphatase localization procedures of Barka and Anderson (1962).

For electron microscopy, small pieces of liver were fixed in 3% glutaraldehyde in 0.1 M phosphate buffer, postfixed in 1% osmium tetroxide for 2 h, and dehydrated in a graded series of ethanol over a period of 1 h. Tissue was embedded in Maraglas according to the procedure of Freeman and Spurlock (1962). Thin sections were cut on an LKB Ultratome, stained in uranyl acetate and lead citrate, and examined with a Siemens Elmiskop. Thick sections were mounted on glass slides and stained with toluidine blue (pH 11.1).

Observations and discussion — The channel catfish liver includes many histologic features that are quite similar to those in hepatic tissue in largemouth bass (Hinton et al. 1972), lamprey (Elias and Bengelsdorf 1952), and trout (Simon et al. 1967). Thus the presence of a dual plated muralium of anastomosing cords of hepatocytes is a common feature. The catfish hepatic parenchyma consisted of continuous masses of cells forming laminae (Fig. 1, 2, and 3). Blood sinusoids were suspended in this labyrinthine, laminar mass (Fig. 3). Hepatocyte nuclei (one per cell) contained

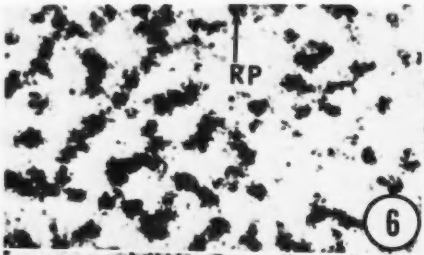


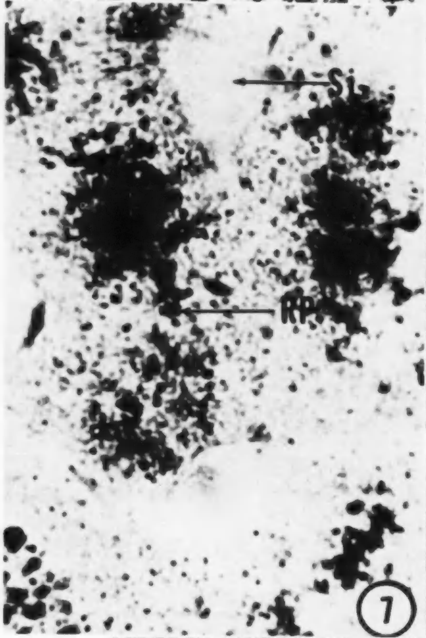
FIGURES 1–5. Histology of liver, including exocrine pancreas (EP)

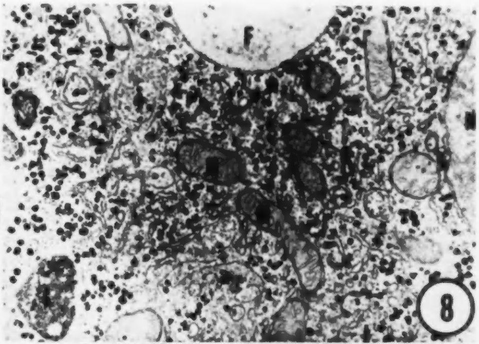
FIG. 1. Portal vein (PV) is surrounded by EP tissue that is basophilic and stains darkly with PAS reagent. Tributaries of the central vein (CV) are not ensheathed by exocrine pancreas. PAS + H. × 380; FIG. 2. EP is shown in close association with the portal vein in which nucleated blood cells (B) are shown. Exocrine pancreatic cells exhibit a strongly PAS positive reaction inside some cells (arrow). Single, prominent, centrally located nucleoli are found in each hepatocyte nucleus. PAS + H. × 500, enlarged 1.75 ×; FIG. 3. Hepatocytes are found in laminae, two cells thick, separated by blood sinusoids (Si). The EP thins out and disappears when nearing the termination (T) of the PV. H & E. × 380; FIG. 4. Argyrophilic reticular fibers form a ramifying meshwork that encloses laminae of hepatocytes. In addition, these fibers are found in walls of the hepatic artery (H), PV, EP, and CV. Reticular fiber silver stain. × 380; FIG. 5. Dual plated muralium (Mu) is enclosed in a network of reticular fibers. Reticular fiber silver stain, × 500, enlarged 1.5 ×.

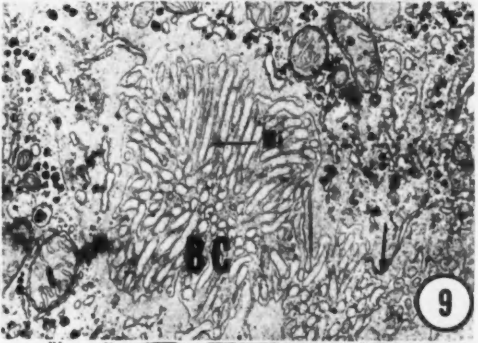
single, prominent centrally located nucleoli (Fig. 2).

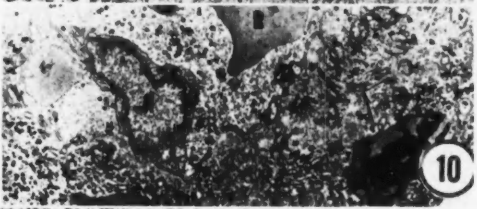
However, differences in hepatic histologic architecture also existed with the presence of dispersed exocrine pancreatic tissue several cell layers thick which surrounded the portal vein, its tributaries (Fig. 1, 2, and 3) and hepatic artery and its branches. These pancreatic acinar cells were larger and more basophilic in H and E stained sections than adjacent hepatocytes and in addition were strongly PAS positive (Fig. 1 and 2). Portal veins could be easily distinguished from central veins since the former were surrounded by exocrine pancreas and the latter were not (Fig. 1). The presence of exocrine pancreatic tissue near portal veins and hepatic arteries in catfish liver qualifies this tissue as dispersed pancreas according to Kristal's (1946) classification. The

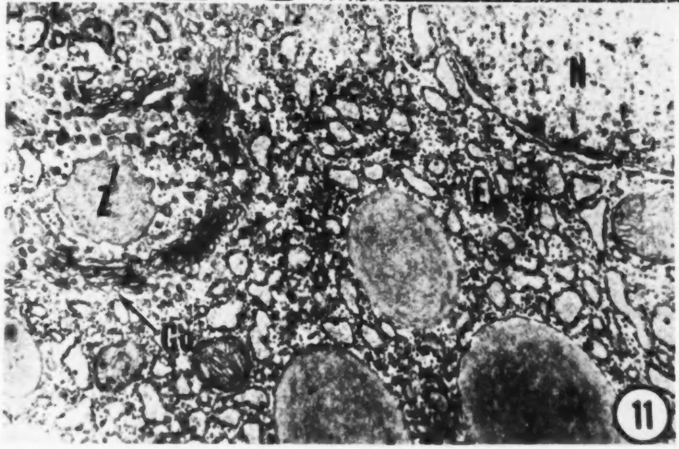

RP
6


S1
RP
7


F
8


M
BC
9


10


N
Z
E
Go
11

PAS positive material seen in histologic sections of exocrine pancreatic cells probably consisted of stained zymogen granules since these granules were observed in electron microscopic sections. The large amount of granular endoplasmic reticulum that occurred in these cells is indicative of their main protein synthetic function, i.e. zymogen granule formation.

Reticular fibers, demonstrable with the silver method, were seen throughout the hepatic parenchyma (Fig. 4 and 5) and formed a meshwork around laminae of hepatic cells. Reticular fibers occurred in walls of sinusoids, blood vessels, bile ducts, and pancreatic acinar tissue (Fig. 4). Also, collagen bundles were seen in perisinusoidal spaces in EM sections. Alterations of these connective tissues in rats and mice (Popper et al. 1961) in response to carbon tetrachloride toxicity are commonly found. In catfish, more attention at the ultrastructural level to connective tissue alteration in response to chlorinated poly-halogenated toxicity seems appropriate.

Acid phosphatase activity was localized to reaction product arranged in a peribiliary canalicular pattern (Fig. 6 and 7). The reaction product was probably contained in lysosomes since acid phosphatase occurs in these structures. The close association of lysosomal-like dense bodies near bile canaliculi is consistent with positive histochemical localization of acid phosphatase near these areas since lysosomes contain acid phosphatase and occur in a peribiliary canalicular fashion (Hinton et al. 1973). Lysosomes are structurally altered in response to toxic dosages of methyl mercury (Verity and Reith 1967), and therefore may serve as sensitive indicators for heavy metal pollutants and thus relate directly to water quality.

The electron microscopic features of the channel catfish liver agreed with those observed with the light microscope. The cytoplasm of the hepatocyte contained filamentous mitochondria, granular endoplasmic reticulum, and glycogen (Fig. 8). Catfish liver cells contained dispersed rosettes of glycogen unlike the clumped glycogen observed by Hinton et al. (1972). Also, the endoplasmic reticulum in catfish was not organized into a perinuclear "cuff" (such as occurs in largemouth bass) but appeared more randomly organized in the cytoplasm. Round, membrane-bound bodies resembling lipid droplets were occasionally observed. Polymorphic, densely staining bodies that closely resembled lysosomes were a constant cytoplasmic component. These bodies consisted of a dense, granular portion and a light, finely fibrillar element.

Biliary canaliculi were situated between hepatocytes (Fig. 9). The canaliculi are expansions of the intercellular space into which microvilli project from the surfaces of the hepatocytes. The microvilli are numerous and sometimes nearly fill the canaliculi with tight junctions joining the hepatocytes near the borders of the canaliculi. Bile canaliculi are minute canals that travel between hepatocytes throughout the parenchyma. In mammals, the electron microscope has shown that the lumen of the bile canaliculus is merely an expansion of the intercellular space and its walls are local specializations of surfaces of adjoining hepatic cells (Rouiller 1956). Similar observations were noted in catfish and also the presence of numerous microvilli projecting into the canalicular lumen was a common finding.

Sinusoids were lined by endothelial cells (Fig. 10). The attenuated processes of these cells had fenestrations 350 Å to 700 Å wide. Macrophage-like cells were not observed lining the sinusoidal epithelium. A perisinusoidal space (Space of Disse) lay between the sinusoidal epithelium and the hepatocyte. Microvilli extended from the hepatocyte into this space. Collagen fibrils (about 500 Å in diameter) were often observed in the perisinusoidal space which probably accounts for

FIGURES 6–11. Histology of liver continued, including histochemistry and electron microscopy FIG. 6. Acid phosphatase reaction product (RP) is localized to areas between adjacent cells within laminae of hepatocytes. Barka and Anderson (1962) method, × 460; FIG. 7. Reaction product (RP) is found in dense accumulations near biliary areas between cells. This is termed a peribiliary canalicular pattern, and indicates acid phosphatase localization in organelles (probably lysosomes) in these areas. Barka and Anderson (1962) method. × 1,250, enlarged 2.8 ×; FIG. 8. Electron micrograph of a hepatocyte. Note the dispersed rosettes of glycogen (G), nucleus (N), fat droplets (F), mitochondrion (M), and lysosome (L). × 17,500; FIG. 9. Electron micrograph of a biliary canaliculus (BC) with microvilli (Mi) projecting into the lumen. Note the tight junction (arrow). × 19,800; FIG. 10. Electron micrograph of a perisinusoidal region. Note the collagen fibrils in the perisinusoidal space (arrow), nucleus of sinusoidal endothelial cell (N), sinusoidal space (S), and red blood cell (R), lysosome (L), and fat droplet (F). × 10,500; FIG. 11. Electron micrograph of an exocrine pancreatic cell. Apparently a zymogen granule (Z′) is being formed by coalescence of material from the Golgi (Go), and larger zymogen granules (Z′) are seen in various stages of formation. Note the tubular, granular endoplasmic reticulum (E). × 10,000.

the positive reticular staining seen in this area with the light microscope.

Electron microscopy confirmed that exocrine pancreatic tissue was dispersed within the liver. Exocrine pancreatic cells were filled with tubular elements of granular endoplasmic reticulum, free ribosomes, and Golgi bodies (Fig. 11). The exocrine pancreatic cells were also identified by numerous zymogen granules that contained material of intermediate electron density, were membrane bound, and about 1–2 μ in diameter. These zymogen granules appeared to be formed from the Golgi and excreted at the apical border of the cell.

Acknowledgments — Support for this research was provided by HEW-PHS-3-S01-RR05386 through the University of Mississippi Medical Center. We thank Mrs R. Cheek, Miss C. Foster, and Mr E. Jernigan for processing and sectioning material for light and electron microscopy.

BARKA, T., AND P. J. ANDERSON. 1962. Histochemical methods for acid phosphatase using hexazonium pararosaniline as coupler. J. Histochem. Cytochem., 10: 741–762.

BULLOCK, G. L., D. A. CONROY, AND S. F. SNIESZKO. 1971. Bacterial diseases of fishes, p. 1–151. *In* S. F. Snieszko and H. R. Axelrod [ed.] Diseases of fishes. T. F. H. Publications, Jersey City, N.J. 151 p. (part 2A) and 41 p. (part 2B).

CHANG, J. P., AND S. H. HORI. 1961. The section freeze-substitution technique. I. Method. J. Histochem. Cytochem. 9: 292–300.

ELIAS, H., AND H. BENGELSDORF. 1952. The structure of the liver of vertebrates. Acta Anat. 14: 297–337.

FREEMAN, J., AND B. A. SPURLOCK. 1962. A new epoxy embedment for electron microscopy. J. Cell. Biol. 13: 437–443.

HINTON, D. E., M. W. KENDALL, AND B. B. SILVER. 1973. Use of histological and histochemical assessments in the prognosis of the effects of aquatic pollutants, p. 194–208. *In* J. Cairns and K. Dickson [ed.] Biological methods for the assessment of water quality. American Society for Testing and Materials. STP 528, Los Angeles, Calif. 256 p.

HINTON, D. E., R. SNIPES, AND M. W. KENDALL. 1972. Morphology and enzyme histochemistry in the liver of largemouth bass (*Micropterus salmoides*). J. Fish. Res. Board Can. 29: 531–534.

HOGAN, J. W., AND C. O. KNOWLES. 1968. Degradation of organophosphates by fish liver phosphatases. J. Fish. Res. Board Can. 25: 1571–1579.

JUDD, C. E., AND F. B. CROSS. 1966. Tissue damage in livers of channel catfish *Ictalurus punctatus*, raised on artificial diets in ponds. Trans. Kans. Acad. Sci. 69: 48–57.

KRISTAL, J. 1946. The exocrine pancreatic tissue of seven teleosts. S. Afr. J. Med. Sci. (Biol. Suppl.) 11: 79–86.

LILLIE, R. D. 1965. Histopathologic technique and practical histochemistry. 3rd ed. McGraw-Hill, Inc., New York, N.Y. 00 p.

MCMANUS, J. F. A., AND R. W. MOWRY. 1960. Staining methods, histologic and histochemical. Paul Hoeber, Inc., New York, N.Y.

OLSEN, O. W. 1967. Animal parasites, their biology and life cycles. Burgess Publ. Co., Minneapolis, Minn. 431 p.

POPPER, H., F. PARANETTO, F. SCHAFFNER, AND V. PEREZ. 1961. Studies on hepatic fibrosis. Lab. Invest. 10: 265–290.

ROUILLER, C. 1956. Les canalicules biliares. Étude au microscope electronique. Acta Anat. 26: 94.

SCARPELLI, D. G. 1967. Ultrastructural and biochemical observations on trout hepatoma, p. 18–24. *In* Trout Hepatoma Research Conference Papers. U.S. Dep. Health Educ. Welfare, U.S. Dep. Inter. Res. Rep. 70.

SIMON, R. C., A. M. DOLLAR, AND E. A. SMUCKLER. 1967. Descriptive classification on normal and altered histology of trout livers, p. 18–24. *In* Trout Hepatoma Research Conference Papers. U.S. Dep. Health Educ. Welfare, U.S. Dep. Inter. Res. Rep. 70.

TAYLOR, N. S. 1965. Histochemical studies of nephrotoxicity with sublethal doses of mercury in rats. Am. J. Path. 46: 1–21.

VERITY, M., AND A. REITH. 1967. Effects of mercurial compounds on structure-linked latency of lysosomal hydrolases. Biochem. J. 105: 685–690.

WILLIAMS, W. L. 1960. Hepatic liposis and myocardial damage in mice fed choline-deficient or choline-supplemented diets. Yale J. Biol. Med. 33: 1–14.

PERSPECTIVES

The Fisheries Research Board of Canada — Seventy-Five Years of Achievements[1]

W. E. RICKER

Contents

1466 ABSTRACT
1466 RÉSUMÉ
1466 PREFACE
1467 INTRODUCTION
1468 FAUNA AND FLORA
1469 STRUCTURE AND FUNCTION
  Anatomy and development
  Biochemistry
  Physiology
1470 SENSES AND BEHAVIOR
1471 DISTRIBUTION AND MOVEMENTS OF FISH STOCKS
  Atlantic region
  Pacific region
  Salmon
  Arctic and inland regions
1473 FISHERY MANAGEMENT
  Dynamics of fish stocks
  Atlantic region
  Pacific region
  Inland region
1477 MARINE MAMMAL MANAGEMENT
1477 FISHING GEAR AND TECHNIQUES
1478 PARASITES AND DISEASES
1479 HANDLING AND STORAGE
  Handling and transferring fish
  Refrigerated and frozen storage
  Transportation and display
  Flavor and spoilage
  Inspection of fish and of processing plants
1480 PROCESSING AND PRODUCTS
  Smoking
  Salting and drying
  Canning
  Reduction
  Other processes
1482 ARTIFICIAL PROPAGATION AND ENHANCEMENT
  Release of fry
  Pond rearing and supplemental feeding
  Spawning channels
  Hatchery techniques and selective breeding
  Transplantation and acclimatization
  Other measures
1484 AQUACULTURE AND LIVE HOLDING
  Fish
  Oysters
  Crustaceans
1485 THE AQUATIC ENVIRONMENT — OCEANOGRAPHY AND LIMNOLOGY
  Atlantic region
  Pacific region
  Arctic region
  Estuaries
  Inland region
1487 POLLUTION
  Industrial and domestic wastes
  Effects on aquatic animals
1488 ACKNOWLEDGMENTS
1490 REFERENCES
1488 APPENDIX

---

[1] La version française est en préparation.

Printed in Canada (J3713)
Imprimé au Canada (J3713)

Abstract

RICKER, W. E. 1975. The Fisheries Research Board of Canada — seventy-five years of achievements. J. Fish. Res. Board Can. 32: 1465–1490.

The idea of having government research supervised by a group of knowledgeable individuals outside of the government service began, in Canada, in the field of aquatic science and fisheries. In 1898 an honorary Board of Management was set up to establish and manage a biological station on the Atlantic coast. As this Board's responsibilities increased it was renamed the Biological Board of Canada, and finally the Fisheries Research Board of Canada. Starting in 1973 the Board ceased to have direct responsibility for the management of research stations, but it continues as an advisory body.

During the period 1898–1972 the Board has provided facilities for original research on aquatic animals and plants and on the waters they inhabit, much of it done by scientists from universities and museums; it has solved many problems faced by governments in locating, evaluating, managing and increasing fish stocks; and it has assisted the fishing industry with improved techniques for catching, handling, processing and marketing its products. The immediately useful results of the Board's work have been made available to the Canadian community through reports, publicity and personal contacts. Details of scientific discoveries have been published in the Board's *Journal* and other outlets, while results of research done in other countries have been sifted and interpreted for their application to the Canadian scene.

Accepted April 22, 1975

Résumé

RICKER, W. E. 1975. The Fisheries Research Board of Canada — seventy-five years of achievements. J. Fish. Res. Board Can. 32: 1465–1490.

L'idée de confier à un groupe d'individus compétents en dehors de la fonction publique la supervision de la recherche gouvernementale prit naissance, au Canada, dans le domaine des sciences aquatiques et des pêches. En 1898, on établissait un office de gestion honoraire chargé de fonder et de gérer une station biologique sur la côte de l'Atlantique. Les responsabilités de cet office allant en s'accroissant, on lui donna le nom d'Office de biologie du Canada et enfin celui d'Office des recherches sur les pêcheries du Canada. A partir de 1973, l'Office a cessé d'avoir la responsabilité directe de la gestion des stations de recherche, mais il continue comme organisme consultatif.

Durant la période 1898–1972, l'Office fournit les facilités nécessaires à la poursuite de recherches originales sur les animaux et les plantes aquatiques, et les eaux qu'ils habitent, une bonne partie étant effectuée par des scientifiques attachés à des universités ou des musées; il résolut plusieurs problèmes auxquels les gouvernements eurent à faire face en ce qui a trait à la localisation, l'évaluation, la gestion et l'accroissement des stocks de poissons; il a de plus aidé l'industrie des pêches avec des méthodes améliorées de capture, de manutention, de transformation et de commercialisation de ses produits. Les résultats d'intérêt immédiat des travaux de l'Office furent transmis à la communauté canadienne par le biais de rapports, publicité et contacts personnels. Les détails des découvertes scientifiques ont été publiés dans le *Journal* et autres publications de l'Office, alors que les résultats des recherches effectuées dans d'autres pays ont été examinés minutieusement et interprétés en vue de leur application au contexte canadien.

Accepté le 22 avril 1975

Preface

The concept of managing government research through an honorary board, made up largely of nongovernment scientists, began in Canada in the field of aquatic sciences. In 1898 a Board of Management was set up in fisheries and marine research, which by Act of Parliament became the Biological Research Board of Canada in 1912 and the Fisheries Research Board of Canada in 1937. This concept was adopted by other organizations in Canada and throughout the world in the belief that research management might be best fostered through the counsel of scientists unconnected with government.

On January 1, 1973 the Fisheries Research Board ceased to have direct *responsibility for the management of research and became an advisory body evaluating Canada's effectiveness in fisheries and marine science. This new role for the Board is challenging and some 10 major studies now in progress will be published within the next year.*

I think it is important that the achievements of the Board over its 75 years of active research be highlighted. And I am indeed grateful to Dr W. E. Ricker, who has served the Board for many years in various senior positions, for summarizing these accomplishments.

J. R. WEIR
CHAIRMAN

Introduction

IN 1898 a Board of Management, consisting of university biologists and a representative of the Ministry of Marine and Fisheries, was established to construct and manage a moveable Biological Station that the Government of Canada had authorized for the Atlantic coast. In 1904 it also assumed partial responsibility for a freshwater Station at Go Home Bay on an island in Georgian Bay, Ontario. In 1908 it was decided that the Atlantic Station should be established permanently at St. Andrews, New Brunswick, and in the same year a Station was founded at Nanaimo, British Columbia. In 1912 the Board of Management became the Biological Board of Canada, operating under a special Act of Parliament. It continued to manage the two marine stations, but the Georgian Bay Station became inactive after 1913. In 1924 the Board's membership was broadened to include representatives of the fishing industry and a wider spectrum of academic expertise, and two Technological Stations were established, at Halifax, Nova Scotia and Prince Rupert, British Columbia. In 1937 the Board's name was changed to the Fisheries Research Board of Canada, and has remained so ever since. In 1973, however, it became an Advisory Board, and direct management of the Stations was assumed by the Fisheries and Marine Service of the Department of the Environment. Meantime several new stations and field laboratories had been founded, moved, or discontinued, and the Fisheries Laboratory of the Government of Newfoundland was incorporated into the system in 1949. A list of stations and laboratories is given in an Appendix.

Throughout the 75 years considered here the Board's operations have served two main functions: (1) to provide facilities for original research on aquatic animals and plants, and (2) to solve problems faced by governments in fishery management, and by the fishing industry in catching, processing, and marketing their products. The year 1925 is a convenient division point when emphasis shifted from the first of these objectives to the second, although there was no sudden change: practical problems were studied from the very first years of operation, and much exploratory research continues; many projects, indeed, serve both functions. For the most part the undirected research was performed by volunteer investigators, usually from universities or museums, while more practical problems have been handled mainly by Board employees. But here too there is no sharp distinction; for example, during the first decade Prof A. P. Knight undertook and solved several practical management problems, and studies of fish products and processing began as early as 1915. What follows is a brief record of some of the more important results of the Board's efforts from 1898 through 1972, including investigations begun during that period but completed somewhat later.

Research work, which investigates the unknown, must by its nature leave behind it many hypotheses disproved, many promising leads that did not pan out. These cannot be regarded as mistakes or failures, because they all add to knowledge, and some have averted costly commitments in unprofitable directions. However, it is natural to dwell on the inspirations that have succeeded, and while negative results are not entirely ignored, this account is frankly biased in favor of success.

Much of the work of the Board was done with the cooperation and support of other sectors of the Department of Fisheries and Department of the Environment, particularly Resource Development, Conservation and Protection, Statistics, Inspection, Industrial Development and Marine Sciences, as well as facets of several other Ministries. Also, some investigations have been made in cooperation with the fisheries administrations of one or more of the Provinces, international fisheries commissions, or the fishing industry.

The results of the Board's work have been communicated to those interested by personal contacts, committee work, demonstrations, memoranda, newspaper publicity, popular brochures and bulletins, manuscript reports, and scientific publications. About half of the printed output has been in the Board's own publications, the rest in outside magazines, books, and journals. Both types are listed in two comprehensive indexes (Carter 1968, 1973). Material published by the Board has included a scientific Journal containing research results, Technical Reports for data records and matters of restricted interest, and popular or scientific Bulletins summarizing work done in a particular field. Two series of Progress Reports and several series of Circulars have been used to bring results quickly to public notice. There are also three series of Manuscript Reports, and a Translations Series containing more than 3000 important foreign works translated either by Board staff or by others. The Board's primary publications have been open to manuscripts from authors anywhere in Canada or abroad who work with aquatic organisms or their environments, including fields in which the Board itself has not been active — for example, fishery economics.

For reasons of space, names of scientists have usually been omitted in what follows, and the names of Stations are used only sparingly. Exceptions are individuals who have written comprehensive monographs, and a number of retired or deceased investigators whose names are prominently associated with some particular field of enquiry.

Fauna and Flora

Collecting and identifying Canadian aquatic animals and plants began in the 19th century or even earlier, but such work received an impetus when the Board's Biological Stations were established. At each of the five sites where the peripatetic Atlantic laboratory was located a strong effort was made to obtain as many kinds of organisms as possible, including of course the fish. The same was true of the Go Home Bay Station during 1901–13, and of the Pacific and Atlantic Biological Stations from 1908 onward. New areas were brought under study during the Hudson Bay expeditions of 1920 and 1930, the investigations of prairie lakes and waters of the National Parks during the 1920s, Newfoundland waters from the Bay Bulls laboratory starting in 1930, arctic and subarctic lakes and rivers in 1944–45 and again more recently, and arctic marine waters starting in 1947.

Although there is now information concerning all the groups of animals and plants of our three oceans and the inland waters, we are still far from having a complete catalog of Canadian aquatic life. Even the fishes are incompletely known; new records for our area turn up almost every year, and as recently as 1967 a new species of rockfish was described that exists in commercial quantities off the Pacific coast. Recently the traditional tools of classification have been increased by several biochemical tests (blood and muscle proteins, enzymes, and isozymes) that supplement the morphological characters used to separate species, varieties, and individual stocks.

Studies conducted at the Board's Stations have contributed substantially to a number of compendia and monographs of particular groups. The Board in fact projected two "Fauna" series of publications, one for each coast, that were intended eventually to include the whole of the animal kingdom. Although this proved to be too ambitious a project, the treatment of Pacific polychaete worms by E. and C. Berkeley is still a standard guide to that group. The hydroids of both coasts and of the arctic have been described exhaustively in three monographs and many papers by C. McLean Fraser. Molluscs too have been a favorite object of study, especially at the Pacific station: its first Director, the Reverend G. W. Taylor, had a fine collection, and several subsequent investigators have greatly extended his work. There are now handbooks of edible molluscs, intertidal bivalves, and marine borers, all by D. B. Quayle. Shrimps, crabs and other crustaceans have been intensively studied, so that the kinds that occur in all our oceans are known rather well. There is a monograph of the arctic sea stars. Other marine invertebrate groups have received varying amounts of study; none has been completely ignored. Finally, there are comprehensive treatments of the seaweeds of both the east and the west coast.

In fresh waters, E. M. Walker's summers on Georgian Bay and at both the Nanaimo and St. Andrews Stations contributed to his monographs of the dragonfly genera *Aeshna* and *Somatochlora*, and eventually to the three-volume Odonata of Canada. No other Order of insects had been treated so fully, although major contributions to the classification and distribution of Canadian midges, phantom midges, caddis flies, mayflies, and stoneflies have appeared, also molluscs, crayfish, water mites, and other groups.

The Board's major concern, however, has always been our fish resources. Its collaborators and employees have contributed importantly to fish systematics and distribution, and it has published several distributional monographs that now cover almost the whole of the country. The first of these concerned the fishes of the Pacific coast, by W. A. Clemens and G. V. Wilby (1946 and 1961), later superseded by J. L. Hart's Pacific fishes (1973). For the Atlantic the first comprehensive publication was by A. H. Leim and W. B. Scott in 1966, although the marine fishes of Nova Scotia had been treated in 1935 by V. D. Vladykov and R. A. McKenzie. Authoritative popular handbooks of the freshwater fishes of British Columbia have been prepared by J. R. Dymond in 1932 (game fishes only), and by G. C. Carl and collaborators (1948–59), the latter published by the Provincial Museum of British Columbia. A monograph of northwestern freshwater fishes by J. D. McPhail and C. C. Lindsey appeared in 1970. In eastern Canada the Board's freshwater work contributed to several local studies, while a comprehensive account of the freshwater fishes of the whole of Canada was published by W. B. Scott and E. J. Crossman in 1973. In the arctic, the fishes of Hudson Bay were described by Dymond and Vladykov in 1933, and a comprehensive treatment of the arctic marine fishes is under way. A book review in Nature (November 1974) compliments the Fisheries Research Board for its most creditable publishing record on fish and fisheries, and states: "By commissioning a series of excellent publications on the fishes of the major geographical regions of Canada, published in its Bulletin series, it has made the Canadian fish fauna the best documented in the world."

Structure and Function

The professors and students who came to the early biological stations included investigators of all the principal biological disciplines. Sometimes they merely brought to the seaside a research project that had engaged them at home, but usually they took advantage of the living material available in the surrounding waters, and quite often their work would be focused on species of economic importance.

Anatomy and Development

A few detailed anatomical and histological studies have been done at the Stations, for example on the pancreas of the skate, the thyroid gland of salmon, the digestive tract of the Atlantic oyster, or the musculature of a Pacific shrimp. One of the most interesting discoveries, due to A. A. Berkeley, was the fact that shrimps change sex: they mature in their second year as males, and in their third year become functional females. Similarly the maturation, spawning, egg and larval development of herring, goldeye, salmon, lobsters, crabs, various molluscs, and other animals have been described by H. I. Battle and many other investigators.

Comparative anatomical studies have been useful in identifying stocks: for example, the counts of the number of scales or vertebrae in trout, cod, haddock, herring, and pilchards made by a number of investigators, and V. D. Vladykov's monograph of the skulls and caudal skeleton of Pacific salmon. So too the number of eggs and the size of the eggs in salmon have been shown to vary not only in relation to the size of the fish, but also between stocks independently of size.

Biochemistry

The fascinating variety of form and structure observed in aquatic animals is matched by an equally fascinating diversity of chemical composition. Many contributions to "biochemical anatomy" have come from the Board's establishments, for example a systematic study of the sterols in major marine Phyla. A similar study of steroid hormones in fish resulted in the isolation of a hitherto unknown blood steroid, 11-ketotestosterone. The principal basis of marine life is phytoplankton and seaweeds, and these have recently been made the subject of intensive biochemical study.

Nor is comparative biochemistry without its practical aspects. The steroid hormone mentioned above has been found effective in promoting the growth of cultured fish. Various enzymes, tissue proteins, hemoglobins, and other substances have been used to distinguish closely related species of fish, or different stocks within the same species. Similarly biochemical tests can distinguish cod fillets from haddock, or turbot from halibut, much more certainly than it can be done by taste and much more easily than by microscopic examination. Other studies have identified enzymes and substrates that produce compounds having unpleasant odors after the fish is killed, which can guide a search for effective preservatives.

Physiology

Physiological work too has great intrinsic and comparative interest, as well as practical importance. In the early days several investigators worked with the production and action of insulin in fish, which provided part of the background leading to its clinical use in man. However, the work in physiology done at Board establishments has been mainly in the fields of nutrition, energetics and tolerances.

Conditions of temperature, salinity, food supply, etc., have been studied that make possible fastest growth consistent with economical utilization of food, particularly for salmon and trout. Different diets and additives have also been tested; for example, it was found that addition of androgens increases growth of salmon.

The swimming ability of anadromous fishes has been of special importance in relation to their chances of surmounting natural or artificial obstructions in a river. Experiments have determined the maximum swimming speeds of several species of salmon and steelhead trout at different temperatures, both in short bursts and at a sustainable rate. Not only species, but different stocks of the same species, were found to differ in this respect.

Another aspect of the migrations of salmon and trout investigated by the Board is their energy expenditure during the long weeks or months of the journey upriver. During the 1920s it was found that stocks of salmon from tributaries near the sea are useless for transplantation upriver, and 30 years later it was confirmed that they lack the energy reserves necessary for long migrations. Similarly, sexual maturation is keyed to the normal migration time, and unusual delays can be harmful. Each major tributary of a large river has its own group of genetically distinct stocks, distinguished by a different range of morphological characteristics and of physiological performance. At the Vancouver Laboratory difference in swimming performance has been related to a particular genetic allele in the steelhead trout. Swimming speeds and endurance of groundfish have also been determined, in relation to the pattern of their avoidance or capture by a moving trawl net.

Knowledge of the tolerance of adult or larval animals to different combinations of environmental factors can help to explain year-to-year variations in reproduction. Thus, the success of hatching and of fry survival in Pacific herring and several groundfishes has been determined for combinations of temperature, salinity, and oxygen content of the water. Similar work with adult lobsters at St. Andrews has indicated the range of variation in these factors consistent with successful live holding.

Senses and Behavior

Fish have all the same senses as man, and apparently one or two extra. Their vision is not the best because their eyes do not have very good resolution, but every angler knows that they can see what goes on both in the water and in the air above. The underwater vision is sensitive at low light intensities, and at Nanaimo advantage was taken of this fact to design a system of moving cables to guide salmon smolts into a bypass away from dangerous turbines.

Most fish have good hearing, and the sensitivity spectrum for cod has been measured in detail. Trials at the St. Andrews Station showed that the noises made by a trawler and by the trawl itself can be detected by cod in a mile or more away. Fortunately, this does not scare them off — in fact, rather the reverse. The behavior of fish at the mouth of a moving trawl was studied using special photographic equipment. Fish may also produce their own sounds; for example, in the course of their reproductive behavior cod and haddock make loud sounds produced by drumming muscles attached to the swim bladder.

It is in their sense of smell, however, that fish really excel: they detect and react to dissolved substances in extremely minute concentrations. It was found that less than one part per billion of the amino acid L-serine, found in mammalian skin, is detected and avoided by migrating salmon, so that simply putting a hand in the water at the head of a fish ladder will cause the fish to turn back. Nor was detection of this scent impaired by large doses of odorous mixtures such as pulpmill effluent.

During the first three decades of this century there was an acute controversy about a salmon's ability to return to its native stream. There was great reluctance to credit the fish with such (as it seemed) impossible behavior, even though populations of salmon spawning in different rivers and even in different tributaries were in many cases found to be quite distinctive morphologically. However, the fact of homing has been established by numerous marking experiments done by the Board and others on both Atlantic and Pacific salmon. There is of course always some straying, varying from less than 1% for sockeye to 10% or more for pink salmon. At the other extreme, A. A. Blair observed an Atlantic salmon that returned to the same identical redd on two successive occasions.

Proponents of homing had long suspected that the sense of smell was involved, and the first experiment to test this was performed in 1925 by E. H. Craigie. He found that normal sockeye tagged in Seymour Narrows reached the Fraser River region 2.6 times as frequently as those with severed olfactory nerves, while 4 times as many were recaptured upriver beyond New Westminster. More recent work has confirmed the role of smell, and has shown that the odor of the home stream is detected and remembered by salmon all through their marine life, so that they choose it on their return to fresh water. The correct time of migration, however, has been found to be mainly an hereditary characteristic so that, for example, where both an early and a late run of salmon occur in the same river system, the progeny of early fish are found to return early in the season, and late-run spawners produce late-run progeny. Even transplantation to a new environment at the egg stage changes this timing very little if at all.

However, a salmon needs more than a good sense of smell to get out to sea a thousand miles or so and then back to where it was born. Board studies on sockeye leaving lakes showed that they orient themselves by reference to the sun or the polarization of the clear sky when it is in view, but switch to an as yet unidentified mechanism in cloudy weather or when swimming at a depth. The same senses may be used in navigation on the high seas.

Another aspect of behavior is the interaction between individuals, which makes fish of some species defend territories, while others assemble in schools. Studies of both have helped to define the carrying capacity of rivers and lakes for desirable species. Changes in behavior are of particular interest; for example, the onset of "smoltification" — changes in morphology and behavior that occur when a young salmon goes to sea — has been advanced by using an artificial regime of change in day length, which can improve the survival of pond-reared salmon after release.

Distribution and Movements of Fish Stocks

For animals of actual or potential commercial importance, it is desirable to learn what exactly is their distribution by area and by depth at different times of year; in particular, where and when they occur in usable concentrations. In the traditional fisheries for species such as cod and salmon this information was well known to fishermen, at least in relation to standard types of gear. But as markets for previously unused species opened up, and as larger vessels and new gear became available, there was need for systematic information on the abundance and catchability of potentially valuable species over the whole expanse of our oceans and fresh waters.

ATLANTIC REGION

While the Biological Stations have engaged in exploration for fish from the very beginning, there has also been a series of special efforts. The Canadian Fisheries Expedition of 1914–15, manned jointly by Norwegian and Canadian scientists, worked mainly in the Gulf of St. Lawrence, mapping stocks of herring and making extensive oceanographic observations and plankton collections. It had been planned to cover a much wider area, but the work was cut short by the First World War. However, the utilization of herring lagged, and from 1944 to 1950 another intensive study of the Gulf and adjacent waters was undertaken by Canada, Newfoundland, Quebec, and the Maritime Provinces, with headquarters at the St. Andrews Station. This revealed the seasonal distribution of certain stocks and suggested methods of exploitation that could take advantage of them. Later it was found that large numbers of herring that spawn in the southern Gulf of St. Lawrence move to southwestern Newfoundland in winter, where they supported a major fishery.

During the 1930s the Newfoundland Laboratory used a chartered trawler to explore the banks and channels in the vicinity of the island. It located several large populations of American plaice and haddock along the southern Grand Bank. Detailed mapping of the distribution of marine fishes became a major part of the Board's work as soon as suitable vessels became available after 1946, part of it being done in cooperation with the Industrial Development Service. Major discoveries by W. Templeman and colleagues include stocks of redfish in deep water all around Newfoundland, cod in deep water off Labrador, Greenland halibut and roundnosed grenadiers off Labrador and Baffin Island, redfish living pelagically beyond the continental shelf and north to Greenland, capelin on the southern Grand Bank and in Trinity Bay, and local stocks of witch flounder, Greenland halibut, and others. Most of this work was done with trawls, but it was also demonstrated that good quantities of large cod could be caught by longlining some distance off the Newfoundland coast, where they were concentrated along a deep temperature boundary. Among invertebrates, stocks of scallops, bar clams, shrimps, snow crabs, and red crabs have been revealed by exploration.

For most species, especially cod, haddock, and herring, the regions inhabited by semidiscrete stocks have been delimited by tagging, as have their seasonal movements, particularly into and out of the Gulf of St. Lawrence. Of particular interest for management was the discovery that in some cases the same stock of cod or herring was being fished in two different places, so that the rate of utilization was greater than had been supposed.

PACIFIC REGION

On the Pacific coast similar explorations have been made. Stocks of Pacific cod and several flatfishes were distinguished, mainly at shallow to moderate depths, and the spawning migrations of these fish were revealed by tagging programs. In deeper waters, the distribution of ocean perch and other rockfishes near the edge of the continental shelf has been mapped from western Alaska to Oregon, but particularly in Queen Charlotte Sound and Hecate Strait. The potential annual yield of ocean perch from these latter areas is estimated to be greater than the total catch of groundfish taken by Canadians off British Columbia in 1972. Usable stocks of shrimp have been located in several areas, which should support a fishery of probably 5 times the present, and there are promising results of explorations for the larger "prawns" in mainland inlets.

SALMON

In both the Atlantic and the Pacific oceans the distribution and migration of salmon have been a complex and an exciting field of research. Up to the 1920s salmon were generally considered to be coastal species. Some said that they rarely left the region where the influence of their native river was dominant. On the Pacific this extreme view became untenable after 1926, when tagging experiments directed by C. H. Williamson showed that chinook salmon bound for the Columbia and Sacramento rivers occurred in large numbers all along the British Columbia coast. A decade later Japanese fishermen found three species of salmon in commercial quantities all the way from Hokkaido to the eastern Aleutian Islands and into the Bering Sea. The Japanese fishery was interrupted by the war, but it was resumed on a large scale shortly afterward within the structure of a treaty that limited its activity to waters west of 175°W long. This "abstention principle" was meant to protect fully exploited North American stocks of salmon (as well as halibut and herring), but there was provision for annual review under the auspices of the newly formed International North Pacific Fisheries Commission. Since the line of division was subject to negotiation, it became necessary to learn exactly where salmon of the different stocks of five species spent their time while out at sea. Scale characteristics and morphometry were of some value, and salmon were tagged at sea and recaptured in coastal fisheries or in fresh water. However, the most revealing evidence came from a discovery by the Nanaimo Station that there were a few parasites peculiar to Asiatic and American salmon, respectively. This made is possible to identify the continent of origin of some fish positively, and in the case of one parasite even a particular river system. Today it is known that the ocean distributions of Canadian sockeye and chum salmon overlap to some extent with the same species from Kamchatka. Considering Asian and North American stocks together, five species of *Oncorhynchus*, plus the steelhead trout, can be taken right across the Pacific south to a temperature boundary at about 14 C.

A perennial problem that became more acute during the 1960s is the interception of Canadian salmon by United States fisheries, and vice versa. Tagging and marking studies have provided the factual basis for the difficult negotiations in which Canada seeks to minimize such interceptions and to ensure an even exchange with the unavoidable remainder.

For Atlantic salmon a similar picture emerged during the 1960s when a major fishery developed off west Greenland, beginning in coastal waters and then extending to the high seas. Again tagging, of smolts in this case, showed that salmon of two continents were intermingled, and more recently good estimates of the proportions of Canadian and European fish taken have been made each year using biochemical characters. A special feature is the fact that only the salmon that spend two or more winters in salt water are taken by this fishery; salmon that return to the river after only one winter apparently do not move so far north. This meant that the reduction in the relative abundance of large salmon in our rivers was greatly accelerated. Representations based on this kind of information have been successful in reducing the number of salmon taken pelagically, and ICNAF agreements call for cessation of the high-seas fishery by 1976.

ARCTIC AND INLAND REGIONS

In 1920 and again in 1930 expeditions were sent to Hudson Bay to find whether it contained commercial concentrations of food fish, and if not, why not. None were found, unfortunately, because in spite of its comparatively southern latitude the Bay becomes cold enough in winter to freeze the blood of ordinary marine fishes. The useful fish in the Bay are brook trout, arctic char, and ciscoes which can retreat into rivers each winter, and a considerable population of capelin.

In 1947 the *Calanus* series of expeditions to the eastern arctic began. They were named for the research vessel built specially for the job, which in turn was named for a copepod that is a basic food of many marine fishes. Collections of fishes and invertebrates were obtained, oceanographic observations were made, and seals and walrus were studied around Baffin Island and in northern Hudson Bay. This work has been continued by the Arctic Biological Station, which later undertook similar studies in the western arctic. Both the eastern and western approaches to the arctic receive enough water from the adjacent oceans that a number of cold-tolerant flounders and cods can exist in populations of moderate size. In the inshore waters of Coronation Gulf as many as four species of cod occur, generally maintaining separate habitat areas characterized by differences of temperature and salinity. However, throughout the arctic the char is the species preferred both by local residents and by visitors.

In inland waters less exploration was necessary, and in any event freshwater fishes are under provincial jurisdiction in most Provinces. However, after World War II the Board sponsored a 2-year study of the large northern lakes and rivers to assess their fishery potential. Great Slave Lake proved to have large stocks and good productivity, so a commercial fishery was established that now yields about 5 million pounds a year. Other waters were much less productive, but some are now being fished. Twenty years later a series of somewhat smaller and more northern lakes were surveyed over several summers, and a special productivity study was made of a small lake on Victoria Island.

Fishery Management

Dynamics of Fish Stocks

A major aspect of the Board's work over the years has been investigations to support or to improve the management of our fisheries. Ideally, this includes estimating the size of each stock, the fraction of it that is taken each year by Canada and by other nations, its rate of replenishment from growth and from new recruits, effects of utilization on the age and size of fish caught, variations in recruitment from year to year, and forecasts of abundance and of catches in the case of stocks that fluctuate rapidly. When fishing becomes intensive it is necessary to consider also the interaction between different stocks and different species — either as competitors for food or a predator and prey. A further problem is to know how many adult fish are needed to obtain adequate recruitment, averaging out the years of favorable and unfavorable environmental conditions. To all of these aspects of population dynamics Board scientists have made major contributions.

In 1918 A. G. Huntsman demonstrated quantitatively how fishing reduces the average age and size of fish in a population and, if recruitment remains the same, also the abundance of the stock. Although he had been anticipated by a Russian scientist 2 years earlier, Dr Huntsman's was the first description in a western language of the "fishing-up effect" that provides the key to understanding the historical development of most fisheries. Large initial catches and excellent fishing success persist while the accumulated stock of old fish is being fished up. When it is gone the fishery must depend on current additions, and the size of these annual recruitments then assumes major importance. Not only that, but whenever overfishing has occurred, the process of restoration of an older age structure requires that catch per unit recruitment must be less than the sustainable level for a number of years after the optimum rate of exploitation is achieved — and this is always a painful process.

As if this were not enough, a Board scientist later discovered that, quite apart from the fishing-up effect, during the later part of a period of increasing rate of fishing the catches available at any rate of exploitation, or from any given number of adult spawners, are greater than with stable or decreasing fishing, and particularly so when stocks having different natural productivities are fished in common. These effects are most evident if the fish are caught only in their final year of life, and they explain the apparent reduction in productivity of many runs of Pacific salmon.

The number of recruits added to a commercial stock each year depends partly on climatic conditions in the water at time of spawning and during early life. Progress has been made in identifying conditions favorable for each species, and hence making predictions of future catches, but much remains to be done. The other factor controlling the number of recruits each year is the size of the spawning stock. The Board's investigations have shown a variety of recruitment patterns, including the discovery that at intermediate stock sizes the absolute number of recruits can be much greater than when spawners are either abundant or scarce. This explains why the fishing-up effect of the previous paragraph is sometimes smothered out — as the older stock is reduced, there is a compensating increase in the number of recruits. However, this pattern does not always occur, and in any event there must be a limit to it. If a spawning stock is reduced too much, the result is too few recruits, which at different places and time has happened in various stocks of salmon, herring, pilchards, and groundfishes. To obtain maximum yield from whatever recruits are available, the corresponding best minimum size and best rate of fishing are determined by the balance between growth rate and natural mortality rate in the stock, and used as a guide for mesh-size regulations.

In order to make such analyses, it was first necessary to assemble information on growth, mortality, and rate of fishing in a number of stocks — not an easy task when the fish are out of sight for most of their lives. Methods of estimating growth rate were under active development during the first two decades of the century, and a Canadian contribution was C. McLean Fraser's modification of proportionality calculations from scale annuli to allow for an initial interval before the scale was formed. Methods of censusing fish populations were developed or adapted for use in Canada by D. B. DeLury and others, particularly the "change-in-fishing-success" and "mark-and-recapture" methods. Widespread tagging of cod, haddock, herring, and the various flatfishes and salmons has provided information on the abundance of major stocks, though much care has been needed to adjust for incomplete reporting and numerous other systematic errors. A general review of problems and techniques in fish population dynamics, published by the Board, has become a textbook on the subject throughout the world.

ATLANTIC REGION

Although our eastern groundfish, particularly cod, have been the object of international exploitation for several centuries, it is only in the last 25 years that this has become intensive enough to require conservation regulations. In 1950 the International Commission for the Northwest Atlantic Fisheries (ICNAF) was established. Canada played a prominent role in this, and the first headquarters of the Commission was at the Board's St. Andrews Station. The Commission has brought together the statistics and research results of all the nations that fish in the region from west Greenland to the eastern United States, it has increased mesh sizes of the nets used in order to release small fish, and it recently established national quotas. However, groundfish research by Canada and Newfoundland began much earlier, in the 1920s and 1930s. Much of it was exploratory in nature, as described previously, but the age structure, growth, and movements of a number of stocks were determined at that time.

Cod continues to be the major food fish taken off our eastern coast. Some 12 principal stocks have been identified, based on many years of biological sampling and tag returns. Haddock, pollock, redfish, and the various hakes and flatfishes have been similarly studied. In all, 59 fish stocks, including 18 species of all ecological types, now have international quotas set by ICNAF. All quotas and other regulations are reviewed every year, requiring a major input from research activities on which to base a suitable figure.

Species such as the haddock off Newfoundland and Nova Scotia, and the redfish in the Gulf of St. Lawrence, reproduce well only in occasional years and the Board's surveys make it possible to predict periods of abundance and scarcity in the fishery. Similar but less extreme fluctuations affect other species. Board surveys also made it possible to forecast the progress of the "fishing-up effect" mentioned earlier, with its inevitable decrease in average size of the fish caught, so that the industry could make necessary adjustments in processing and packaging.

The rapid expansion of the Atlantic herring fisheries since 1960 has created special management problems. Canadian Atlantic herring catches increased from less than 100,000 tons in the late 1950s to more than 500,000 tons in the mid-1960s. Management was then complicated by the entry of foreign nations, so that total removals from herring stocks in the whole of the northwest Atlantic were close to a million tons in 1968 and 1969, and then declined to around 500,000 tons. Temporarily large removals are of course characteristic of a fishing-up period, but recent recruitments have been disappointing and there is a great danger that spawning stocks have become too small to provide adequate reproduction. Most herring stocks are now under quota control designed to rebuild them to optimum levels. There have also been qualitative changes. Recent large concentrations of herring off southwestern Newfoundland have been mainly of the autumn-spawning variety hatched in the southern Gulf of St. Lawrence, which perform annual migrations into and out of the Gulf. During the 1940s herring in the same region were mostly from local spring-spawning stocks. The present (1972) stocks consist mainly of the dominant year-class spawned in the fall of 1958 and spring of 1959, whose success may be related to the vacuum left when Gulf herring were reduced by a fungus disease during 1954–56.

Atlantic salmon have always been a small, though valuable, part of the eastern commercial fishery, and a major prize for sportsmen. Marking experiments on the Little Codroy, Miramichi, and Petitcodiac rivers showed that the rate of commercial utilization of salmon larger than grilse was 75% or more even before the Greenland fishery began, while anglers might take 50% or so of the remainder. Other studies have defined the number of spawners needed in major streams, and their carrying capacity for parr and for presmolts, while electrofishing methods were developed for ascertaining the actual number present. These are now in routine use: for example, to assess the effects of pollution, or the tempo of recovery from overfishing. Somewhat earlier, experiments were performed with artificial freshets to bring salmon into small rivers for summer angling, but results were marginal and scarcely justified the costs.

Board scientists played a major role in the development of fisheries for large pelagic fishes off the east coast. Surveys indicated that swordfish stocks were underexploited, and the demonstration of new harvesting techniques and new areas of distribution contributed to a quadrupling of the swordfish harvest from the 1950s to the 1960s. Unfortunately, this fishery has been abandoned, at least temporarily, because of a natural mercury content of the flesh that is above present acceptable tolerance levels. Evidence was also obtained on the abundance and seasonal distribution of bluefin tuna and skipjack off eastern North America. This led to the development of a sport fishery in the Gulf of St. Lawrence, and to a commercial tuna fishery based in New Brunswick which is now mainly pursued in the eastern tropical Pacific and off the west coast of Africa.

The lobster fishery is characterized by many local stocks inshore, all intensively exploited using baited "pots," as well as a more scattered population in deep water. The Board's first management-oriented work with lobsters was to establish the best minimum size for maximum economic return in different areas, and to specify the lath spacing on the pots that would permit most of the "shorts" to escape. This meant getting estimates of the rate of growth and natural mortality rate, for which ingenious tagging methods were evolved. Another problem is that of mechanical raking for Irish moss (a seaweed), which was shown to kill an appreciable number of lobsters. Recently the snow crab and the red crab have become economically marketable, and they present a set of problems somewhat similar to those for lobsters.

Other commercial invertebrates occur offshore and present management problems similar to fishes, including international regulation. For the scallops of the Bay of Fundy and Georges Bank, oceanographic and biological studies have explained year-class variability and established data for regulations. In Newfoundland the squid is a valuable bait species, but is subject to extreme fluctuations in availability from year to year. Exploratory fishing on the Grand Bank can be used to forecast abundance 2 months in advance, and methods of capture less labor-intensive than the traditional jigging have been demonstrated.

Many other eastern fisheries and fisheries have been studied by the Board, with resulting improvement in management techniques: for example smelt, shad, alewives, eels, hake, cusk, witch and winter flounders. One general management problem is that more and more we are "fishing down the food chain" — that is, taking large quantities of small abundant species like capelin and herring which are a major food supply for larger animals such as cod and harp seals. Soon it will be necessary to set priorities, and this will require both biological information and politico-economic decisions.

PACIFIC REGION

The Pacific fisheries of Canada have been dominated by the five kinds of salmon, halibut, and herring. Recently other species have been increasing in importance, but the narrowness of the western continental shelf means that groundfish and crustaceans can never assume the dominant position they have in eastern Canada. Studies on the growth, migrations, etc. of salmon and halibut were begun during the first years of the Pacific Biological Station by J. P. McMurrich and A. Willey, and herring studies were instituted by C. McLean Fraser; however, the halibut investigations were turned over first to the Provincial Government and in 1923 to the International Fisheries (Halibut) Commission. Work on salmon and herring continued without interruption by Dr Fraser and others, while other species were soon added; for example lingcod, rockfishes, chabs, clams, kelp, and sea lions. Both for salmon and for herring the basic management problem has been to know how many spawners are needed to produce a maximum harvest — which is a different thing from maximum recruitment, although at first this was not realized.

During the 1920s and 1930s Board work with Pacific salmon was mostly concerned with migration, artificial propagation, and enhancement of stocks, as described elsewhere. However, a special study of the Cowichan River system by Ferris Neave and others provided data for management of its trout and salmon populations. Another important study was the systematic sampling and reporting of the size and age compositions of sockeye salmon in the major fisheries, year by year. This series, begun for the Provincial Government in 1914 by C. H. Gilbert and continued after 1924 by W. A. and L. S. Clemens at Nanaimo, has been indispensable for interpreting changes in the sockeye fisheries and in the fish themselves, and for setting present rates of utilization.

During the postwar period the Board mounted a major investigation of salmon production in the Skeena River system and less intensive work in other watersheds, except that since 1938 the International Pacific Salmon Fisheries Commission has had the responsibility for studying the sockeye, and later the pink salmon, of the Fraser River. Additional marking and tagging experiments were done at various locations, both in fresh and in salt water, to further define migration routes and to estimate rates of utilization, which are the basis of present management policy. A crisis interlude occurred in 1951 and 1952, when a rock slide on the Babine River obstructed the migration of most of the sockeye in the Skeena system. Cooperative investigations with the Fisheries Service revealed the extent of the damage and the means for remedying it. A little later, studies of young sockeye and limnological work at Babine Lake showed that most of the numerous fry produced in its outlet river did not move into the main body of the lake, which accordingly had a sparse sockeye population and a large surplus of plankton food. This led to the construction of two large spawning channels that have greatly increased smolt production from the lake and subsequent commercial catches.

The problem of dominance, or extreme differences in the size of successive generation lines of some sockeye salmon runs, is of great scientific and practical interest, and Board scientists were the first to suggest reasonable explanations for the phenomenon. In the case of Fraser River sockeye it involved a predator–prey interaction between young salmon and trout, and this now has support from studies done by the Salmon Commission at Shuswap Lake. On the Skeena and most other rivers there are two important ages of maturity for sockeye, which complicates any interaction and makes extreme dominance unlikely.

Next to halibut the Pacific cod is the major groundfish species used in British Columbia. As compared with more northern stocks, our fish grow fast and have a rather short life span, and substantial fluctuations in year-class strength make for a fluctuating fishery. Recently a technique of reading the scales was developed making it easier to assess the condition of the stocks. Other groundfish have also been studied in greater or less detail, and the results used for setting fishing seasons, quotas, closed areas, and trawl mesh regulations. Management of Dungeness crabs had had considerable attention, and the fact that the males are much larger than the females has made it a much easier task to set and enforce a useful size limit than in the case of lobsters.

Herring research was first concerned with their age structure and its change as the fishery developed. The numerous stock units along the British columbia coast were distinguished and mapped during the 1930s and 1940s from morphometric characters, and tagging later provided an estimate of the interchange between these units. Life-history studies during the 1950s showed that the abundance or "strength" of each brood is established during the highly vulnerable egg and larval stages, demonstrating the need to preserve the quality both of the shoreline and of the inshore waters. Pacific herring, unlike those of the Atlantic, spawn near the low tide mark, so that a semiquantitative estimate could be developed of the amount of spawn produced each year, and hence of the number of spawners. From this and from the age structure of the catch, the Nanaimo Station makes annual estimates of the supplies that will be available to the fishery. This made it possible to recommend the relaxation of restrictions on the reduction of herring in the 1930s, because ample supplies were then available. Unfortunately, Board plans to ascertain the optimum rate of utilization by intensively fishing a limited area were twice "shot down," so that when continued improvements in the efficiency of fishing eventually resulted in overexploitation during a period of poor fry survival, almost the whole coast was affected, and several years of closure were necessary to bring the stocks back to a reasonable level. During the 1960s the major offshore feeding grounds of herring were located by midwanter trawling and sensitive echo sounders. These were mainly within 50 miles of the coast, and it proved possible to protect them from most foreign fishing through international negotiations.

INLAND REGION

In 1906 the Station at Go-Home Bay first addressed itself to problems of the exploitation and management of freshwater fisheries. Studies were made on the sizes of trout and whitefish taken in gillnets, and the fate of fish caught and released — stimulated by the problem of capture of small trout in whitefish nets. After this Station closed, the Board during the 1920s continued to support studies of the ciscoes, whitefish, and other species in the Great Lakes, in cooperation with the Ontario Fisheries Research Laboratory. Studies of prairie lakes were made from a Biological Station located at Gimli on Lake Winnipeg in 1929 and 1930. Other management studies were conducted on trout lakes of Jasper National Park by A. Bajkov and F. Neave, in the Kamloops region of British Columbia by C. McC. Mottley and D. S. Rawson, and on lakes and ponds of New Brunswick and Prince Edward Island by M. W. Smith. These showed that major factors limiting trout production can be either predators (eels, fish-eating birds), or competitors (minnows), or the large old trout themselves.

After the Second World War the new Winnipeg station worked with freshwater management problems, particularly the new fishery on Great Slave Lake, where annual sampling for size, growth, catch, and fishing effort provided the basis for annual quotas of lake trout and whitefish. Less detailed studies provided a scientific basis for managing Great Bear, Tathlina, Kakisa, and other lakes in the Northwest Territories, and contributed to provincial management practices on lakes Winnipeg and Manitoba. A study of the goldeye through most of its Canadian range revealed its peculiar life history, notably that it has floating eggs, which are unusual among freshwater fishes. These studies in turn contributed to rational management of the species in the delta areas of several large rivers and their associated lakes.

During the 1940s the sea lamprey invaded the Great Lakes above Niagara Falls, where it quickly reduced the stocks of lake trout in lakes Huron and Michigan to commercial extinction and was well on the road to this in Lake Superior. International action to control the invaders was implemented, and the Board carried the Canadian part of the work during its experimental stages. Electrical barriers on spawning rivers killed most adult lampreys but not quite enough, and were abandoned in favor of a poison that kills lamprey larvae but, in the concentrations used, not the fish. The task of reestablishing lake trout is a slow one, although good returns are being obtained from fingerling plantings made by Ontario and neighboring states. However, rainbow trout have flourished under the new regime, and more recently coho and chinook salmon have provided excellent sport fishing.

Marine Mammal Management

Marine mammals are a particularly vulnerable resource because of the slow rate of replacement of the stock — commonly of the order of 10% per year. This means that a sustained harvest should be somewhat less than this, but it is very difficult to persuade a competitive industry to exercise such restraint when large numbers of animals are obviously available. As a result a number of Canadian stocks have become extinct or nearly so: sea otters off British Columbia, humpback whales in the Strait of Georgia, walruses on Sable Island and in the Gulf of St. Lawrence, and bowhead whales in the eastern arctic. Others are at a low ebb and are given complete protection by all nations, for example, the blue, grey, right, and humpback whales. Since 1972 Canada has suspended commercial whaling for all species in order to build up their stocks, and eventually a sustained yield will be possible.

The harp seal has survived in fairly large numbers because it was mainly their newborn pups that were harvested and because sealing was, up to recently, a difficult and hazardous occupation. Hooded seals also provide some skins each year, and their stocks too are under international study. Ringed and bearded seals, beluga, narwhal, and walrus are all taken by indigenous peoples. For the former commercial species the Board developed estimates of abundance and mortality rates and traced their migrations, by means of age composition studies and tagging. Similar estimates have been made for the arctic mammals, which are used almost wholly by the Inuit or Eskimos. Brochures on management of ringed seals, white whales, and walrus have been prepared in the Inuit language.

On the Pacific the Board and several cooperating agencies have begun the task of reestablishing sea otters by transplantation of animals from Alaska. Fur seals are a special case because of their polygamy and harem structure. Reduced to a few small herds early in this century, international agreement permitted them to increase to about 2 million animals while surplus young males continued to be harvested on the breeding grounds. Canada shares in the harvest, the Board has had the responsibility of assisting with the research upon which the management program is based. The Board also sponsors an animal census of killer whales — really a large dolphin — of which a few specimens are taken alive each year for display in oceanaria.

Two potentially nuisance species, from the fishery point of view, have received considerable study. These are the sea lions in the west and the grey seals in the east. Sea lions are not utilized at present, but the grey seal is subject to a small controlled kill by the federal government. The skins are used commercially, but the main purpose is to reduce damage to salmon and salmon nets and also to reduce the numbers of a cod parasite that uses the seal as a final host.

Fishing Gear and Techniques

The Board has assisted in developing new types of fishing gear and procedures, and testing those already in use, particularly from the point of view of best utilization of stocks. An early study by A. P. Knight concerned the effects of dynamite, because some fishermen had begun to use dynamite to harvest schooling pollock in the Bay of Fundy. This was found to be wasteful because up to one half of the fish were not recovered, although the range of effectiveness of a stick or two of dynamite proved to be much less than anticipated. A test on a vastly greater scale was available for study in 1958, when Ripple Rock was blown out of Seymour Narrows north of the Strait of Georgia, using 1400 tons of explosives. This great detonation injured fish only within a range of less than half a mile.

One of the methods used to increase Atlantic fish production, starting early in the century, was to install bait freezers so that cod fishing could continue when fresh bait was not available. However, there was at first a great reluctance to use frozen bait because, by experience or by hearsay, it had acquired a bad reputation. In the summer of 1906, when the Atlantic laboratory was stationed at Gaspé, fishing trials were arranged with local fishermen using fresh and frozen herring. These showed that the frozen bait should be thawed in cold water so that it remained firm. In this form it caught somewhat fewer cod than fresh bait at times of slack water, but was superior to fresh bait in strong tidal currents, apparently because it stayed on the hooks better. In time the prejudice against frozen bait disappeared.

On the Pacific coast the Board played a major role in introducing echo-sounding to locate schools of herring, and this quickly replaced taut-wire sensing with resulting increase in efficiency. Later it investigated the use of mercury lights by seiners, and found that they greatly increased the proportion of small herring and salmon in the catches, so that their use was prohibited.

In harvesting clams major problems have been the slowness and expense of hand digging, and the breakage and loss of clams in the process. The Board developed a modified hydraulic clam dredge that was 90% efficient in taking legal-sized clams, while it eliminated the large breakage loss characteristic of digging or using nonhydraulic dredges.

On the Pacific coast midwater trawls were developed that have provided a basis for present commercial models, including a new type of "door" to keep the trawl open. Tests of various types of trawl continue at St. Andrews, both in the laboratory and on the fishing grounds. Data on shapes and stresses of commercial trawls have been obtained from specially devised instruments.

The characteristics of net twines were investigated extensively and the results passed on to fishermen, along with methods of retarding rot in natural fibers. Determination of the fluid mechanics of netting and screens at small angles of flow has corrected early misconceptions about the forces of water on fishing gear.

For winter fishing in fresh water, a simple transmitter has been developed at Winnipeg for locating the "jigger" that carries a line from one ice hole to where a new one will be cut.

Parasites and Diseases

The faunal surveys that were conducted at the early biological stations included cataloging and describing the parasites of fish and invertebrates. Such studies have continued and will continue for many years before a more or less complete species list is available. More important than simple enumeration are the effects of the parasites on their hosts. Some are known to cause considerable economic loss. For example, many young Pacific salmon are killed, directly or indirectly, by the copepods *Salmincola* and *Caligus* and by the tapeworm *Eubothrium*; an oyster disease caused major losses to the Maritimes industry during the 1950s; and a fungus disease killed large numbers of herring in the Gulf of St. Lawrence during 1954–56. Unfortunately, the control of aquatic parasites in nature is a problem that has baffled biologists all over the globe. Best hopes lie in finding or selecting disease-resistant stocks, and this in part is what was done in the case of the oyster disease.

There are also nonlethal parasites that live in the flesh of fish and, without being in any way harmful to man, are objectionable in appearance and so affect the quality of the product. One such is the nematode *Terranova* found in cod and many other marine fishes. A procedure for routine inspection of fillets by "candling" was developed by the Board and has made it possible to avoid large losses, while the present trend toward the utilization of smaller sizes of cod has greatly reduced the prevalence of the parasite in the catch. Another problem species is the plerocercoid stage of the tapeworm *Triaenophorus* that encysts in the flesh of ciscoes and whitefishes, particularly in prairie lakes. This indeed was a principal reason for establishing a research station in Winnipeg following the Second World War. Its studies showed that some lakes have only small populations of *Triaenophorus*, and this plus a system of routine inspection has preserved the market. Ultrasonic detection of the parasite in the flesh of the fish has proved possible. An attack on the natural occurrence of *Triaenophorus* showed that it could be eliminated from a small lake by sufficiently intensive removal of pike, its final host; this has not yet proven practical on a large scale, but work is continuing. A third problem investigated by the Board is that of "milkiness" of the flesh of marine fishes, caused by a myxosporidian parasite.

The growing aquaculture industry has no greater problem than control of contagious diseases among fish or invertebrates held in necessarily crowded quarters. Studies of various diseases of salmonids, lobsters, and oysters are under way at several of the fisheries research stations. Some diseases are not known to occur in Canada while others, such as furunculosis, vibriosis and kidney disease of salmonids, are not yet found throughout the country. To avoid spreading such pests more widely, a control system is being developed for certifying fish as free from important disease organisms and parasites when moved internationally or interprovincially.

In another category are human diseases associated with aquatic products. There are practically no poisonous fishes in Canadian waters, but some of our shellfish on both coasts periodically become toxic by accumulating a poison that is present in one of their food organisms, a species of the protozoan genus *Gonyaulax*.

In the Atlantic this can become harmful seasonally in the Bay of Fundy and the St. Lawrence estuary; in the Pacific it is less common but an outbreak can occur almost anywhere. Two bulletins describe the ramifications of the problem on both coasts, and a monitoring system has been developed that warns the public of dangerous areas and prohibits the marketing of affected species.

A few parasites of Canadian fish can be transmitted to man if the fish are eaten raw, notably the tapeworm *Diphyllobothrium* and the nematode *Anisakis*. Studies have been carried out to minimize the risk of infection in localities where they occur.

Handling and Storage

HANDLING AND TRANSFERRING FISH

The goal of improved quality and longer "shelf-life" of fish products implies the best possible conditions of handling and storage from the time the fish are caught. When the Technological Stations were established, one of the first projects was to improve the storage bins and icing practices on trawlers, and designs prepared by the Halifax laboratory are today still in wide use. The use of aluminum rather than wooden pen boards was particularly useful in reducing both labor and bacterial contamination.

Another concept in vessel storage is to hold fish in refrigerated sea water (RSW) at temperatures slightly below 0 C (31 F). This was pioneered by H. L. A. Tarr at the Board's Vancouver laboratory and has been widely adopted. In our Pacific fisheries RSW is now used extensively, particularly on packers, as a storage medium for salmon. Most components in RSW systems have been standardized, and use of this technique has meant savings of about a million dollars annually. RSW must be used with caution for some species of groundfish, but the more important ones can be stored for reasonable periods. Saturation of RSW with carbon dioxide retards bacterial spoilage and in species such as ocean perch protects the skin color from bleaching to some extent, but has serious detrimental effects if the fish are to be subsequently frozen or canned.

In transferring fish from boat to boat or boat to plant various types of unloaders are used, including pumps whose design was elaborated by engineers of the Vancouver Station in cooperation with industry. In the Pacific fisheries these are being increasingly used: most fish today have been pumped at least once, sometimes twice, by the time they are delivered to the processing plant, and with less damage than is caused by mechanical unloading. Pumping has proved invaluable for rapid unloading of fish from tanks of refrigerated sea water.

REFRIGERATED AND FROZEN STORAGE

After artificial refrigeration had become practical it was quickly applied to fish. In the fall of 1914 Johan Hjort demonstrated in Canada a new Norwegian method of quick freezing of fish. Soon afterward quick freezing of hake was undertaken experimentally at St. Andrews, in response to complaints from Canadian troops that the fish reaching France were tough and tasteless. The experiments showed that hake frozen quickly, held at a low temperature, and cooked soon after thawing differed very little from fresh hake, but to establish these favorable conditions on a large scale in wartime was another matter.

The various aspects of frozen storage were studied at Prince Rupert and Halifax. Different glazes and packaging materials were tested, to retard drying and oxidation of the oil. A device was invented to determine the true freezing point of fish flesh, and extended research on the effects of freezing temperatures on the muscle proteins have become the foundation of the present frozen fish industry in North America, particularly rapid freezing. But long before the theoretical background was complete, in 1929 the Halifax Station developed and marketed a quick-frozen product in standard packages under the name "Ice Fillets." Although they sold at a premium, general utilization of this principle came only much later.

One major problem in frozen storage is to maintain a consistently low temperature — preferably of the order of −30 C (−22 F). Board engineers developed designs for "jacketed" cold storage rooms and assisted with their installation in various plants. Later the same principle was adapted to frozen storage on board fishing vessels, which is now widely used when long storage is expected. For tuna vessels a brine-spray freezing system is available. Freezing units are being continually improved by research done on both coasts. A packaged combination plate and blast freezer has proved very effective in reducing freezing time, thus making it possible to handle a greater volume of fish. Problems of freezing, thawing for processing, and then refreezing, without loss of quality, have been worked out at St. John's, to the great benefit of the trap cod industry in which large temporary gluts of fish are a common occurrence.

Many other special problems have had to be met: for example, lobsters can be held frozen only after preliminary cooking, which must be for long enough to completely inactivate the digestive enzymes.

TRANSPORTATION AND DISPLAY

Unfortunately, holding problems do not end at the processing plant. Board engineers, led by Otto Young, conducted a sustained and finally successful campaign to have railway cars and trucks fitted with individual refrigeration units that would get fresh fish to inland markets in edible condition. The design of adequate storage and display cabinets for fish in retail stores is an accomplishment of the last 25 years or so, to which the Board has made a significant contribution. The attractiveness of the product is important, and a fillet slicer developed by the Board assists by providing fillets of uniform thickness.

FLAVOR AND SPOILAGE

Along with the improvements in equipment there have been studies of the structure and composition of the flesh of different species, related to their nutritive value, texture, and flavor. The source of the "fishy" odor of quick-spoiling species was quickly identified as trimethylamine (TMA), formed by postmortem reduction from the trimethylamine oxide normally present in fish muscle. Recently the compound ethylenediaminetetraacetic acid (EDTA) has been found efficacious in inhibiting trimethylamine production, and when combined with vacuum packing it can double the shelf life of fillets.

Bacterial spoilage has also been intensively studied, C. H. Castell and H. L. A. Tarr being leaders in this work. At the Prince Rupert station sodium nitrite was shown to retard spoilage of fillets, and it is still used in some countries, although considered potentially dangerous if the product might be used incompletely cooked. An aureomycin compound, chlortetracycline (CTC), was found to be a safe and very useful antibiotic when added in minute quantities to the ice used to chill fish. However, eventually this use of CTC was banned in the United States for no valid reason, and at present it is not widely used on this continent.

A deadly but thermolabile poison produced by the bacterium *Clostridium botulinum* can occur, but fortunately very rarely, in improperly processed food products. Although cooking destroys the poison, the Board has studied the nutritional physiology of this organism intensively with a view to reducing the danger to absolute zero.

INSPECTION OF FISH AND OF PROCESSING PLANTS

During the summers of 1921 and 1922 the Board was asked to investigate sanitary conditions in Prince Edward Island lobster canneries. This was done, and an educational campaign was conducted that resulted in improved conditions and better quality of the product. Similar educational work was done unobtrusively in later years from Halifax and Prince Rupert, until in 1945 the Department's Inspection Service was organized not only to take care of plant conditions but to check the quality of fish put on the market. Both aspects of inspection were based on the Board's work on handling and spoilage; in fact the Service's first Director, E. Hess, was a well-known microbiologist on the staff of the Halifax Station.

Processing and Products

The traditional methods of preserving fish for long periods were salting, smoking and drying — singly or in combination. In the last century canning became important, and later the reduction of less valuable species and processing wastes to meal and oil. All these techniques have been the subject of intensive study by the Board to obtain better quality, greater yield, or lower costs through mechanization.

SMOKING

Scientific study of techniques of smoking began at the Atlantic Biological Station in 1915. After 2 years of experimentation with haddock, a superior finnan haddie was produced, said to rival the best from Aberdeen. Later this kind of work was transferred to Halifax. Other species were used, and there was an investigation of the construction and operation of the smokehouse itself. Soon smokehouses of Board design became widely used throughout the Maritime Provinces, with great saving of labor and improvement in the quality of the product. Similarly, there has been commercial application of smoking equipment and procedures developed at Prince Rupert and Vancouver, and at London and Winnipeg for freshwater fishes.

SALTING AND DRYING

One of Canada's oldest industries is the catching and curing of cod, which began in Newfoundland immediately after (some say before) the voyages of John and Sebastian Cabot. But the traditional method of drying the fish on "flakes," though picturesque, is very laborious, so that the salt-fish industry too has gradually adopted mechanization. At Halifax, St. John's, and Grande Rivière intensive studies were made of the salt concentrations in the pickle, length of salting, drying temperatures, and air velocities in the drier, that were required to obtain different types of product. As a result, mechanically dried fish are now rated as equal to the best natural cure, top quality is obtained more consistently and with much less labor, and salt cod has become something of a premium product in Mediterranean countries. More than 200 salt-fish driers of a design developed by the Halifax Station have been installed. Similarly a salt-fish washer engineered by W. A. MacCallum has been widely accepted. Red discoloration of salt fish was traced to bacteria found in solar salt and preventive measures were developed. Other bacteria are kept under control by adequate sanitation in the plant. Bulletins on curing salt fish were prepared by A. G. Huntsman in 1927 and by S. A. Beatty and Henri Fougère in 1957.

Other species besides cod have been preserved by salting. Prior to World War II there was a large market in the orient for dry-salted herring, and the Prince Rupert Station did considerable work on the details of the process.

CANNING

The mechanics of fish canning have been brought to a high level of perfection by industry, but at the time of World War I there were still a few problem areas. One of these was the occurrence of swelled or bloated cans due to bacterial spoilage, which the Board investigated as early as 1916. More extended bacteriological and other studies were made of the blackening of canned lobster and of the cans themselves, now usually avoided by the use of a parchment liner. Another problem was the browning of canned fish caused by the "Maillard reaction," the chemistry of which was worked out at Vancouver. Still others are the "curd" and the crystals sometimes found in canned salmon, which though harmless reduce consumer acceptance, and have been partly overcome as a result of Board investigations.

Recently Board work in canning has been mainly in testing and demonstrating new types of products, particularly from little-used species such as alewives. The difficult problem of predicting the color of the flesh of canned salmon from that of the fresh fish has been solved by cooperative work of the Vancouver Laboratory and the B.C. Research Council. A salmon color sorter is now available for commercial use.

REDUCTION

The fish reduction industry has gone through several phases. On the Pacific coast it originally depended mainly on the great stock of pilchards or California sardines, whose larger members moved north to Vancouver Island in summer. These fish disappeared after the 1940s, but meantime reduction of herring had been legalized. During the 1920s and 1930s the oil was the most valuable product, and the subject of much Board research. This culminated in a comprehensive review by H. F. Brocklesby and O. F. Denstedt in 1933, which was revised and largely rewritten by members of the Prince Rupert Station in 1941, and again brought up to date in 1952 by B. E. Bailey and others. These bulletins dealt exhaustively with marine oils, particularly those of western Canada, including information on extraction, analytical methods, chemistry, and certain nutritional properties.

Cod liver oil has long been used medicinally, but only during the Second World War was the importance of fish oils as a source of vitamin A fully appreciated. There was a brief but intensive interlude of studies to determine the vitamin A and D content of the livers of dogfish and other sharks, lingcod, and halibut, which resulted in a very valuable vitamin oil industry. This subsided when synthetic vitamin A became available in the early 1940s. An extraction process for lipids, developed at Halifax, has been adopted by laboratories all over the world.

In recent years the meal obtained from most kinds of fish has become more valuable than the oil, particularly for animal feeding. Intensive studies were made on the nutritive value of herring meal. Reduction methods were better standardized, bulk handling techniques were developed, and antioxidants were added to improve the storage stability and nutritional properties of the product. The reduction industry has now become important on the Atlantic coast, using herring mainly, but turning also to underutilized species such as capelin, argentine, and sandlance as the accumulated stocks of herring are thinned out.

OTHER PROCESSES

Over the years numerous new preparations and specialty products have been prepared by A. W. Lantz and others in Board laboratories — for example, fish sausages, breaded products, etc., usually with a view to utilizing low-priced species. New products for human consumption are tested by means of taste panels: individuals who are asked to compare flavor and texture of fish handled or prepared in different ways, or to try out previously unused species. The Board's first taste panel was assembled at St. Andrews in 1919, and the technique has been used extensively ever since.

A potentially important product, fish protein concentrate, has so far had only minor success on the market. Although the "Halifax process" produces it more economically than other methods, it is beyond the reach of the populations, mainly in tropical countries, in whose diet it would be a valuable protein supplement. However, a version has now been made for the domestic market that can be used as "binder" in meat products such as sausage, and would increase the animal protein content of these foods. After many unsuccessful attempts, currently freeze-drying of cod steaks has given an acceptable product whose storage characteristics are under study.

Sometimes a new product will "catch on" quickly. The Japanese market for herring roe, long known to exist but not developed by Canada, was opened up a few years ago and has become a very profitable venture. Roe processing techniques similar to those used in Japan were developed at the Vancouver laboratory, which also gave financial support to the development of an instrument for sorting the mature fish by sex.

There are also nonfood products. Up to about 1940 work was done on the properties of pilchard and herring oil as a base for paints. Recently it has been shown that the oils and waxes of the barracudina, a small fish that occurs commonly in the Gulf of St. Lawrence, have the same properties as the valuable sperm whale oil. A purified hormonal preparation (gonadotropin) obtained from the pituitary glands of salmon has been used to stimulate spawning of pond fishes in southeast Asia.

Artificial Propagation and Enhancement

RELEASE OF FRY

Artificial hatching and release of larvae or fry of salmon, trout, whitefish, shad, lobsters, and other species was a standard management technique in Canada and elsewhere during the last quarter of the 19th century and first quarter century of the 20th. Today this practice has largely been abandoned, and where possible it has been replaced by other procedures: either rearing the fish to larger sizes before release, or giving assistance to natural propagation. The Board has played a major role in this change of emphasis. Studies on lobster development and survival between 1913 and 1917 showed that Canadian lobster hatcheries were making practically no contribution to the fishery, and they were closed after 1917. In 1923 a study by H. C. White of the fate of trout fry planted in two small streams revealed a very large mortality during the first summer. In 1925 the Board was asked to assess the contribution of the British Columbia sockeye salmon hatcheries to the fishery, and a 12-year experiment was set up at Cultus Lake under the direction of R. E. Foerster. This showed that hatcheries were contributing very little to the total sockeye production, although for small runs the standard procedure, release of fry, could produce about twice as many adult sockeye as natural spawning did. Accordingly it was decided to close the British Columbia salmon hatcheries. Unfortunately the fiscal pressures of the depression were so great that no alternative management activity was substituted at that time.

For sockeye, as well as most species of salmon and trout, the principal limitation on abundance is the availability of freshwater habitat where they must spend their early life. However, two species of salmon, pinks and chums, go to sea as soon as they emerge from the redds, and at Cultus Lake and elsewhere there was evidence that hardier fry were produced by hatching eggs in gravel rather than in baskets suspended in troughs. After the war this lead was followed up at Nanaimo. The inferiority of trough-reared fry was shown to have both an energy and a behavioral component. On the one hand, the fry swam more or less continuously and lost weight when not separated from each other by stones; and on the other, they lost their inclination to move downstream when they were exposed to light prematurely. Tests with pink salmon hatched and held in darkness in gravel-filled tanks showed that they equalled naturally spawned fry in all respects, including percentage return as adults. At present prices and costs, hatching these species yields a return of several hundred percent, and pilot-scale operations are under way.

POND REARING AND SUPPLEMENTAL FEEDING

Coho, chinook, sockeye, and Atlantic salmon spend several months to several years in fresh water, which makes them adaptable to a more intensive propagation technique: feeding and rearing in ponds until the time for migration arrives. Alternatively, they can be released before migration time into waters not adequately stocked by natural spawning — above impassable falls, for example. The Board conducted extensive experiments with the latter technique using Atlantic salmon, and found that good adult returns could be had only if merganser populations were reduced to a low level on the river of release. Rearing coho and chinook salmon to smolt size in ponds has begun in British Columbia, and experiments are determining the temperature, food regime, and size and time of release that will give best adult returns. Also trials have been made of supplemental feeding of young cohoes in natural streams, and of increasing their natural food supply by adding organic substrates.

SPAWNING CHANNELS

Another management technique is to improve natural spawning beds or construct special channels for natural spawning in situations where existing gravel areas are inadequate. The necessary conditions of gravel porosity, water flow, and oxygen requirements of the eggs were researched at Nanaimo, and experimental channels have now been built at several sites in British Columbia by Resource Development and by the Salmon Commission. At Babine Lake these have been shown to produce fry of normal behavior and hardiness, though the conditions required for maximum percentage hatch are still under study. Indications are that in an average year the channels will add to the harvest at least half a million sockeye valued at more than 3 million dollars, and possibly twice that number.

HATCHERY TECHNIQUES AND SELECTIVE BREEDING

Early experiments at Cultus Lake showed how long sockeye eggs and sperm could be held before fertilization, and recently frozen storage of sperm has had some success. The "sensitive period" during egg development was pinpointed — showing when eggs could be moved without damage. Different methods of taking the eggs were compared. Tests of the number of males needed to fertilize the eggs of a given number of females, both artificially and in nature, showed that a considerable surplus of males is normally available, which opened up possibilities for selective breeding and for the alternative use of those not needed. Selection of the larger individuals for breeding is becoming an urgent matter, because a somewhat heavier utilization of the larger salmon by the fishery favors the survival of slower-growing and of early-maturing individuals, and this has been reducing the average size of salmon caught.

Another artificial measure with potential for the future is to develop superior stocks by hybridization and selection. A start was made during the prewar period when reciprocal crosses were made between the five species of Pacific salmon; all were reared to maturity in ponds and their fertility established. Recent work has been directed at crossing different stocks of the same species to obtain desirable combinations of characters.

TRANSPLANTATION AND ACCLIMATIZATION

Introduction of new fish species, and the transplantation of fish from one part of the continent to another, was a major activity during the early days of fish culture in North America. Results were both good and bad: valuable fish, especially several kinds of trout, have been established where formerly they did not exist; but there have also been unfortunate introductions of predators or competitors into waters that supported more desirable species. The Board and others have made several attempts to introduce lobsters to the Pacific, where there is abundant physically suitable habitat. These have survived and reproduced, but no native stock was established — perhaps because only a few thousand animals were used. Similarly, introductions of Pacific salmon to Atlantic waters have had no permanent success as yet, although there is a nucleus of pink salmon in Newfoundland and cohoes in Maine, the latter from United States liberations.

Stimulated partly by Board thinking and cooperation, Ontario has established pink salmon in Lake Superior and kokanees (freshwater sockeye) in Lake Huron, while both Michigan and Ontario maintain good stocks of cohoes and chinooks in all the Great Lakes by annual introductions.

OTHER MEASURES

Pink salmon mature only in their second year of life, and a pronounced disparity in the size of the run in alternate years is a common, though not universal, characteristic of the species. To establish good runs in the "off" years is an obvious approach to increased catches. About 1930 A. L. Pritchard made several experiments in transplanting pinks to Masset Inlet in the odd-numbered years, which lack native runs in that area. Although good migrations of fry went out to sea in 2 years, there was an almost complete failure of returning adults, showing that something more than absence of spawners is involved in the off-year phenomenon. Three hypotheses seem possible: (1) that the fry of off years are below some threshold number needed to run the gauntlet of predators on their way to the open sea; (2) that there is cannibalism of the young fish on their way out by the returning adults, which has been shown always to favor the more abundant brood and reduce the smaller one; and (3) that there are hereditary differences between the two broods, each being adapted, for example, to a particular feeding ground or migration route. The last hypothesis is now being tested by accelerating the maturation of male pinks and using their sperms to fertilize females from elsewhere. Already off-year stocks that contain ¾ native genes are available, and a field trial will soon be possible.

A trial was made of the usefulness of kokanees from an inland lake to add to the production of anadromous sockeye. Results were disappointing, but the experiment contributed to distinguishing between the fully lake-adapted kokanee and the "residual" sockeye that were the progeny of anadromous parents.

Control of the predacious fishes in Cultus Lake increased natural sockeye production there to 3 or 4 times its normal level, and was economically attractive under the price and wage structure of the 1930s. A new attack on the problem of increasing sockeye salmon production has recently been made by mineral fertilization of a lake very poor in nutrients. Increases in plankton and in sockeye growth and condition have been obtained, which are being reflected in increased commercial catches.

Finally, artificial reefs to increase lobster abundance have been demonstrated successfully in the Gulf of St. Lawrence. The increased yield of lobsters will meet the cost of their construction over a period of a few years.

Aquaculture and Live Holding

FISH

For many years the principal form of commercial pisciculture in Canada was rearing trout in fresh water for market or for private angling. Recently there has been a greatly increased interest in aquaculture of all sorts, and a wide variety of products is under study. Stimulated by successful rearing of Atlantic salmon and trout in Norwegian fjords, several commercial saltwater rearing projects have been undertaken here, with very uneven results to date. On both coasts Board studies are in progress to learn the conditions necessary for consistent success in this field. Most of the available species of trout and salmon are being tried, and there are promising results for coho and sockeye salmon and rainbow trout. By hatching eggs and holding fry in warmed water it has been possible to get an early start on growth for the year, and the use of heated water from electrical generating stations is under study.

Other species of fish are also being tried. Sablefish or black cod have proved very adaptable to culture, but so far the commercial aspects are marginal. In all cases it is necessary to use a diet that gives the product a natural or "wild" flavor and appearance, and taste-panel tests are part of every project.

A very successful innovation by the Board has been the use of prairie pothole lakes to rear trout. These shallow basins are typically so eutrophic that fish suffocate under the ice in winter; at the same time they produce a rich crop of invertebrate food in summer. By stocking limited numbers of fingerling trout in spring it was found possible to obtain fish of half a pound to a pound in autumn, when they are harvested using gillnets or seines. The harvest is delayed until just before freeze-up, when the fish have lost the "muddy" flavor that often prevails during the warm part of the year.

OYSTERS

During the present century the oyster industry changed over from a free-for-all harvesting of wild stocks that threatened to decimate the supply, to a culture technique based on leased grounds. In 1903 and 1904 the mobile laboratory was stationed at the famous oyster locality of Malpeque Bay, Prince Edward Island, and nearly all the investigators studied some aspect of oyster development, physiology or ecology. This work was continued in later years, and was translated into management recommendations by Joseph Stafford in 1913. During the 1930s at the Ellerslie field station, A. W. H. Needler developed the technique of collecting spat on floating substrate (concrete-coated egg-crate fillers), and of rearing during the second year in floating trays, after which they were planted on firm bottom. He also "sold" the local oysterers on the need for leasing grounds to establish adequate control of the harvest. This station's accumulated experience has been summarized in a comprehensive Bulletin by J. C. Medcof, and has recently been applied to commercial ventures on Cape Breton Island.

On the Pacific side a major discovery was a source of abundant seed oysters in Pendrell Sound, which has eliminated dependence on imported seed with its ever-present danger of introducing additional harmful pests. An artificial cultch has been developed that is beginning to replace natural shell for collecting spat. Raft culture of oysters up to commercial size, similar to what has long been practiced in Japan, has been demonstrated as practical in the ice-free waters of British Columbia. This extends the range of oyster production out beyond the intertidal zone, and into pollution-free and nutrient-rich areas of the coast which, though favorable for growth, are too cool for oyster spawning and hence lack natural populations. Bulletins describing both ground and raft culture have been prepared by D. B. Quayle.

CRUSTACEANS

The Canadian lobster industry prospers best when there is a year-round supply of live lobsters that can be sold when markets are strongest. In order to extend the period of availability, lobsters are held alive in floating wooden pens, in shore-based tanks, or in large natural tidal pounds, but there have been problems with all three. In extended storage food must be supplied in suitable quantity to maintain weight without polluting or deoxygenating the water. For good growth lobsters require about 6% of their body weight in food per week at high summer temperatures, and it was found that the food must conform to nutrition standards that were not met by diets formerly in wide use. For short-term storage, where growth and molting are not desirable, somewhat less food will maintain weight. A blood parasite, *Gaffkya*, has sometimes caused large losses, but is not a serious problem if the animals are not under other stress. Given shelters in the form of drain tiles, and suitably cool temperatures, survival is much improved.

Recently red crabs have become commercial and can be held alive like lobsters, preferably at temperatures below 12 C. They also proved resistant to gaffkemia.

The Aquatic Environment — Oceanography and Limnology

No study of aquatic animals and plants is complete without knowledge of the waters in which they live. From the beginning, therefore, attention was given to the physical and chemical characteristics of oceans, lakes, and rivers, and a full-time oceanographer was employed for the Atlantic in 1928 and for the Pacific in 1930. However, several other government departments were interested in the oceans, and from the middle 1930s there was cooperation from the Navy and the Hydrographic Service, particularly in providing vessels for oceanographic observations. To correlate ocean studies there has been a series of interdisciplinary committees, dating back to 1930. One of these became very active during the Second World War, when the Board's oceanographers were drawn into classified research, for example that related to "false targets" caused by density discontinuities. The present name of the coordinating committee is the Canadian Committee on Oceanography. In 1960 the federal government's major responsibility for oceanography was transferred to a new Marine Sciences Branch of the Department of Mines and Technical Surveys, and when the Department of the Environment was formed in 1971, the MSB became part of its Water Management Service. But the fisheries research stations continue to do some of the work directed specifically at fisheries problems.

To be of maximum usefulness oceanography, like meteorology, requires series of observations taken at regular intervals and with standard techniques. Unfortunately, collecting such data is much more expensive on the ocean than on land, but some progress has been made, as described below. Another approach to a continuous systematic description of the ocean environment is to use meteorological records of air pressure. These can be used to calculate wind-driven transport of ocean water over broad areas, which is related to its temperature and content of nutrient chemicals. The necessary computations were developed at the Nanaimo Station, and have shown a promising capacity to predict fish food supplies and to help predict fish catches themselves.

ATLANTIC REGION

A report on the temperature and density of the water in Passamaquoddy Bay was published by the Board as early as 1912. The Fisheries Expedition of 1914–15 provided the first comprehensive picture of the Gulf of St. Lawrence and waters off Nova Scotia. It was followed by a series of studies on smaller areas, some of them related to prospects for oyster culture: the Cheticamp expedition of 1917 studied the area from Cape Breton to the Magdalen Islands, the Miramichi Region was covered in 1918, St. Mary's

Bay in 1921, and St. Margaret's Bay in 1922. The Strait of Belle Isle expedition of 1923 concentrated particularly on the movements of water through that strait. Since the war there has been intensive work in Malpeque Bay in relation to oysters, in the Gulf of St. Lawrence related to the cod and herring fisheries, and in the Bay of Fundy in relation to a proposed tidal power development. Special studies of ocean currents were made by releasing floats and also "sea-bed drifters" that are later picked up by trawls.

Regular temperature series are taken at a number of sites, starting in 1921 for Passamaquoddy Bay. Annual oceanographic observations in depth are made along several transects running offshore from southern Labrador to southern Newfoundland, and quarterly observations along a line off Halifax. These have been useful in predicting catches of cod and haddock during the same year, and in a variety of other ways. The observations in the Gulf of St. Lawrence are used to forecast ice conditions there.

PACIFIC REGION

Accounts of Board work in Pacific oceanography begin in 1916, but the first comprehensive study concerned the Strait of Georgia and estuary of the Fraser River, done during the late 1920s by C. C. Lucas and A. H. Hutchinson. Later Nootka Sound and the Strait of Juan de Fuca were examined, while N. M. Carter made a special study of the mainland inlets. During the 1930s regular seawater observations were instituted by J. P. Tully at a series of lighthouses along the coast; these were expanded after 1945, and in the 1950s and later more varied records were started at the weathership 700 nautical miles west of Vancouver Island. Major surveys conducted since the war were of Barkley Sound in relation to herring production, the Strait of Georgia for a better understanding of physical characteristics and mechanisms of flushing that are important for fisheries and pollution control, Hecate Strait in relation to the spawning of several groundfishes, Dixon Entrance for elucidation of physical processes affecting water characteristics and movements, and the subarctic North Pacific (coastal and pelagic) in relation to the distribution of salmon and other fishes. For Alberni Inlet and Hectate Strait the circulation and other characteristics were studied in detail by means of hydraulic models constructed at Nanaimo.

For some years the experimental study of primary production was a major effort at Nanaimo, which included large polyethylene bags suspended in the ocean as "aquaria." In 1960 this culminated in a major review by J. D. H. Strickland. The same author, with T. R. Parsons, developed new analytical procedures for sea water and modified old ones, leading to a Manual of Sea Water Analysis that is everywhere the standard reference work.

ARCTIC REGION

Detailed oceanographic work in the Canadian arctic began with H. B. Hachey's observations during the Hudson Bay expedition of 1930, which showed that this great body of water was truly Arctic in spite of its southern position. In 1947 an eastern Arctic program began which has included many oceanographic stations, particularly around Baffin Island and in northern Hudson Bay; this work was summarized in 1951 in a comprehensive publication by M. J. Dunbar. The western Arctic region, including the Beaufort and Chukchi seas, was studied cooperatively with the United States starting in 1949, and the icebreaker *Labrador* connected the two areas by an east to west cruise in 1954. In 1962 five field parties and two icebreakers made a special survey of the central Arctic.

ESTUARIES

The oceanography of estuaries is important because they are at once critical for fish production and particularly susceptible to harmful changes. Both adults and young of anadromous fishes and eels must spend some time in them adapting to the change in salinity, and the young must find food there at a critical stage of their life.

Our largest estuary is the St. Lawrence, and the one carrying most salmon is the Fraser; both have been the object of study to learn their contribution to fish production and to identify critical habitats that must be preserved. The Board's first comprehensive study, however, was of Alberni Inlet by J. P. Tully, who published a monograph concerning it in 1949. Estuaries of the Miramichi and St. John rivers in the east, and the Squamish River tributary to Howe Sound in the west, have also received major attention. Recently the Pacific Biological Station and the Pacific Environment Institute, in cooperation with the Marine Sciences Branch, have made special studies of the Squamish and Nanaimo River estuaries, which have resulted in recommendations regarding port development, dredging, etc.

In the East, the Marine Ecology Laboratory has obtained evidence that events in the coastal region play a major role in determining the abundance of fish stocks, even those that live well offshore.

INLAND REGION

Observations on the physical and chemical characteristics of lakes and rivers have been made on nearly all bodies of water where the Board's biological studies have been conducted — including most of the Great Lakes, the large lakes bordering the Canadian Shield from Winnipeg to Great Bear, saline prairie lakes, trout lakes in New Brunswick and in the National Parks of the Rockies, and a number of salmon-producing lakes of the Pacific littoral. In one of the latter, Cultus Lake, year-round observations revealed that in spring the thermocline forms at a depth and rises until a strong gradient is established fairly near the surface — the reverse of the description then given in textbooks. Comparative studies by D. S. Rawson and others showed that the chemical content of fresh waters, as measured by alkalinity, conductivity, or total dissolved solids, is closely correlated with biological production, and together with mean depth was found to be the major determinant of fish yield.

Primary production in fresh waters, as in the ocean, comes from algae and larger plants, and is a special concern of the Board's unit at the Canada Centre for Inland waters. R. A. Vollenweider was the editor and a principal contributor to the International Biological Program's Manual on the subject. Too much primary production leads to accelerated eutrophication, which has become an acute problem in some places, and a major effort has been devoted to its causes and its control. A principal symptom of increasing eutrophication is a decrease in the oxygen content of the deeper waters of a lake in summer, or in winter under the ice. In Lake Erie this has gone so far that the large burrowing mayflies, formerly a major food of useful fishes, have almost been eliminated. A series of lakes in northwestern Ontario has been set aside by the Ontario government for the experimental study of eutrophication by the Freshwater Institute at Winnipeg. For example, various chemicals have been added to different lakes, and their effects on the chemistry and the aquatic life was observed. These studies, together with laboratory experiments and field work on lakes Erie and Ontario, demonstrated that phosphates made the principal contribution to excessive eutrophication and led to restrictions on the sale of phosphate-based detergents. Alternative compounds, that would do much less environmental damage, were tested and (in one case) recommended for use.

Pollution

INDUSTRIAL AND DOMESTIC WASTES

Pollution of natural waters is by no means a new phenomenon. The first volume of papers from the Biological Station, published in 1902, included an article on the effect of polluted waters on fish life, by A. P. Knight. He studied effluents from a pulp mill, a gas works, and a nail factory. A more extended study was made of the effects of sawdust and bark from lumber mills, which at that time were frequently blamed for fluctuations in the catch of both freshwater and marine fishes. Dr Knight was able to show that mill wastes were likely to be harmful only locally on the smaller rivers, and recommended individual regulation in place of the blanket (but largely unenforced) prohibition that then existed.

Since 1900 the load of domestic and industrial effluents has increased enormously, organic herbicides and pesticides have made their appearance, and radioactive wastes have become a potential threat. Much effort has been expended to determine and to reduce their harmful effects on fish. For example, advice from Board scientists has helped to locate recent pulpmills in British Columbia in areas where these wastes would be quickly dispersed, and to improve the waste disposal systems of existing mills. They have also recommended sites for sewage outfalls of several cities on both coasts, in places where they would do least damage.

Where contamination is present, protection of food supplies is essential. For many years the Board has cooperated with the Department of Health and Welfare in devising regulations and closures to ensure that contaminated products do not reach the market. At the same time, studies of the buildup of bacterial loads, and of the mechanism and time required for natural cleansing in unpolluted water, have made it possible to use products harvested alive from lightly polluted areas.

It is desirable that the fishing industry should set a good example in disposal of its wastes. A system of treatment developed at the Vancouver Laboratory is now being installed in many plants, which uses screening as a first stage and flotation as a second.

Sometimes crisis situations arise that demand prompt assessment and action by the Board and other agencies. Some of the major ones have been the epidemic of spraying forests with DDT during the 1950s in New Brunswick, mine wastes in the Miramichi River, the discharge of deadly elemental phosphorus into Placentia Bay, Newfoundland, the spill of Bunker C oil from a tanker into

Chedabucto Bay, Nova Scotia, and the discovery of mercury in toxic quantities in fish living near industries where this metal is used. All these presented major research and administrative challenges. For example, the mercury crisis required a major redirection of effort at the Freshwater Institute, including the development of new methods for determining small amounts of mercury in fish and in the environment. In that connection, it has been found that marginally dangerous levels of mercury sometimes occur naturally, particularly in large oceanic species that feed at the top of the food chain and so get mercury that has been successively concentrated by a series of organisms, starting from the natural level of mercury in sea water. Although such fish could be harmful only if eaten in very large quantities, the ban on their sale has disrupted several fisheries.

EFFECTS ON AQUATIC ANIMALS

Whether large or small, sudden or gradual, crises such as are described above have stimulated intensive work to determine the effects of each pollutant on fish and other aquatic life, including an acceptable safe level when possible. For example, the necessary degree of dilution of sulphate pulpmill effluent was determined to make it harmless to young salmon. Such work involved determining not only direct toxicity, but also sublethal stresses and changes in behavior patterns that make fish less capable of normal growth and survival. For example, it was found that young Atlantic salmon held briefly in dilute copper–zinc mine wastes or in a weak DDT solution showed no immediate effect, but they were only 65–75% as successful as untreated fish in surviving their life at sea and returning to their native river. To predict such effects without an extended field trial, tests of food conversion efficiency and of maximum swimming speed have been devised; for example, stress from certain pollutants was exhibited at only one-thirtieth of the concentration required to cause death. The cortisol content of the blood has been found to be another sensitive index of stress.

There can also be environmental damage that restricts the habitat for fish or reduces their food supply: for example, stream insects are much more sensitive to DDT than are the fish that prey on them, and their disappearance can be almost disastrous to fish as direct mortality of the fish themselves.

Acknowledgments

This synopsis has been prepared from the source documents listed in the References and from original reports of investigations. In addition, in 1974 the views of all the Research Stations and of a number of former Board employees were solicited. Practically all of the suggestions received have been incorporated, and I wish to thank those who contributed. Nevertheless, this is a personal document in the sense that the choice of materials and emphasis must to some extent be colored by my own knowledge and interests; but my hope is that nothing of major importance has been overlooked completely.

Appendix[2]

PRINCIPAL ESTABLISHMENTS OF THE FISHERIES RESEARCH BOARD

Research establishments and field stations of the Fisheries Research Board of Canada and its predecessors, the Biological Board of Canada (1912–37), and the Board of Management of the Marine Biological Station (1899–1907).

The names of establishments have been changed from time to time, and in 1967 the prefix Fisheries Research Board of Canada (here abbreviated as FRB) was added to current names of that year. The following notes are compiled under the titles in use in 1973, or at the time of termination of a station. Substations and field stations are listed under parent units. In 1973 these establishments became part of the Fisheries and Marine Service, Department of the Environment.

1. The "Marine Biological Station" 1899–1907. East coast of Canada.

Variously referred to by E. E. Prince, Chairman of the Board of Management as "Dominion Biological Station," "Canadian Biological Station," and "Marine Station." This station was moved by scow from shore locations: at St. Andrews, N.B. in 1899 and 1900; at Canso, N.S. in 1901 and 1902; at Malpeque, P.E.I. in 1903 and 1904; at Gaspé, Quebec, in 1905 and 1906. The scow sprang a leak while the station was being towed to Sept Iles, Quebec in 1907 and was beached near Grand Vallée. The Station was not used again as such, the season's work being done at Sept Iles in rented accommodation.

2. "Georgian Bay Biological Station," Go Home Bay, Georgian Bay, Ontario 1901–13.

This Station was founded under the auspices of the federal government and for the first 3 years was supported in part by it. Its activities were reported annually from 1902 by E. E. Prince, Chairman of the Board of Management, which assumed full responsibility for it in 1904. It was not active after 1913, and was formally discontinued in 1917. The first federally supported freshwater investigations in Canada were done here.

3. FRB Biological Station, St. Andrews, N.B. 1908–73.

Land for the "Atlantic Biological Station," St. Andrews, was acquired in 1907, and construction of buildings began in 1909. This Station operated mainly seasonally, June–September, until the mid 1920s, when the first full-time scientific staff was employed.

---

[2] Compiled by Dr. L. W. Billingsley.

A field laboratory called the "Biological Substation, Ellerslie, P.E.I.," began in 1929. From 1931–33 it was called the "P.E.I. Marine Station", and from 1934–41 the "P.E.I. Biological Station." Since then the original name has been used.

3(a). The "Atlantic Oceanographic Group" (AOG) was administered by the Atlantic Biological Station from 1946 until transferred to Halifax in 1960, and to the Bedford Institute of Oceanography at Dartmouth in 1962. The AOG was the Atlantic coast unit (under H. B. Hachey) of the Joint Committee on Oceanography. This Committee, formed in 1946 to coordinate the interests of several federal departments, in 1959 became the Canadian Committee on Oceanography. In 1965 the AOG became part of the Marine Ecology Laboratory, Dartmouth. (The Pacific Oceanographic Group was a similar unit on the west coast, formed at the same time [under J. P. Tully].)

4. FRB Biological Station, Nanaimo, B.C. 1908–73.

Established as the Pacific Biological Station, Nanaimo, construction of buildings was started in 1908. It was operated seasonally until the 1920s, as was the Atlantic Biological Station.

The "Biological Substation, Cultus Lake," B.C. was operated from 1925–38, for salmon research.

The "McClinton Creek Sub-station," Graham Island (near Masset, B.C.) was operated from 1934–42, for pink salmon research.

5. FRB Halifax Laboratory, Halifax, N.S. 1924–73.

Established in 1924 as the "Fisheries Experimental Station (Atlantic)" at Halifax, it was renamed "Atlantic Fisheries Experimental Station" in 1934, "Technical Station, Halifax" in 1955, and FRB Halifax Laboratory in 1967.

It was responsible for the "Eastern Passage Laboratory", Halifax, from 1927–36.

The "St. John's Technological Unit" was operated by it from 1949 to 1972.

From 1966 to 1970, it operated the station at Grande Rivière, Quebec, under the name "Technological Station," Grande Rivière.

6. FRB Vancouver Laboratory, Vancouver, B.C. 1924–73.

Established at Prince Rupert, B.C. in 1924 as the "Fisheries Experimental Station (Pacific)," renamed "Pacific Fisheries Experimental Station" (Prince Rupert), 1934, and relocated in Vancouver in 1942 as the "Pacific Fisheries Experimental Station" (Vancouver). Subsequently it was known as (in 1955) "Technological Station, Vancouver"; (1962) "Technological Research Laboratory"; (1966) "FRB Technological Laboratory"; and (1967) "FRB Vancouver Laboratory." It has a detachment located in the Pacific Environment Institute (see 12).

Vancouver Laboratory administered the Technological Unit, London, Ontario from 1964–66.

7. Gaspé Fisheries Experimental Station, Grande Rivière 1936–66.

Administration transferred in 1966 to Halifax Laboratory, which operated it as a Technological Station until 1970, when it was closed.

8. FRB Freshwater Institute, Winnipeg, Manitoba 1944–73.

Originating in part as the "Central Fisheries Research Station" in Winnipeg in 1944, this became the "Biological Station, Winnipeg" in 1955, and the "Biological Station, London" Ontario, from 1957 to 1966.

8(a). In 1955 the "Great Lakes Sea Lamprey Control Investigation" set up a Temporary Station at Sault Ste Marie. In 1957 this became the "Biological Station, London" for researches on the Great Lakes, replacing "Biological Station, Winnipeg" and the lamprey control headquarters in Sault Ste Marie. It operated Substations at Hay River, N.W.T., for Great Slave Lake; also one at Heming Lake; and lamprey control at Sault Ste Marie.

8(b). The "London Technological Unit" was formed in 1955, and shared quarters with the "Biological Station, London" until 1966, when both became part of the new "FRB Freshwater Institute" in Winnipeg. It was administered from 1964 to 66 by Vancouver Laboratory.

8(c). The Sea Lamprey Control Experimental Station in Sault Ste. Marie, built in 1965, was staffed from Biological Station, London in summer 1965, and in July 1966 was transferred from FRB to the Department (of Fisheries and Forestry).

8(d). Under the Winnipeg or London Biological Stations, the North West Fisheries Investigations, 1944 became Great Slave Lake Investigation, 1944–47, and Mackenzie River and Great Bear Lake Investigations.

8(e). Also, the Eastern Arctic Fisheries Investigation (1947–49) in Ungava Bay became the "Arctic Biological Station" in the 1960s.

8(f). A Great Lakes Unit, maintained at Burlington, Ontario, in the Canada Centre for Inland Waters, became a separate establishment in 1972.

8(g). Although the Board did not operate a freshwater station between 1914 and 1943, it conducted many studies on inland waters. These included: the Jasper Lakes Investigations of 1925–26 and the Prairie Provinces Investigations of 1927–33, with use of a laboratory at the University of Manitoba; support for certain investigations of the Ontario Fisheries Research Laboratory during the 1920s, which were subsequently continued by the Winnipeg station. Research on both freshwater and anadromous fishes in eastern and western lakes was also carried on by the St. Andrews and Nanaimo stations.

9. FRB Biological Station, St. John's, Newfoundland (1949–73).

Formed from the Newfoundland Fisheries Station (1930–48) when Newfoundland joined Canada, it became one of the FRB establishments in 1949. It took over the "St. John's Technological Unit" in 1972.

10. FRB Arctic Biological Station, Ste. Anne de Bellevue, Quebec 1955–73.

This station developed as the "Arctic Unit (Montreal)" in 1955 from the Eastern Arctic Fisheries Investigation (see 8e) and became the "Arctic Biological Station," in Montreal, in 1963. In 1965 it was relocated in Ste. Anne de Bellevue.

11. FRB Marine Ecology Laboratory, Dartmouth, N.S. 1965–73.

Formerly the Atlantic Oceanographic Group (see 3a) this establishment is located in the Bedford Institute of Oceanography.

12. Pacific Environment Institute, West Vancouver, B.C. 1971–(1973).

The Pacific Oceanographic Group, based at Nanaimo from 1946 to 1971, became part of the Institute in that year.

13. FRB Great Lakes Biolimnology Laboratory, Burlington, Ontario 1972–73.

Formerly the Great Lakes Unit of the Freshwater Institute, it became an independent establishment in 1972, and shares accommodation in the Canada Centre for Inland Waters.

Carter, N. M. 1968. Index and list of titles, Fisheries Research Board of Canada and associated publications, 1900–1964. Bull. Fish. Res. Board Can. 164: 649 p.

1973. Index and list of titles, Fisheries Research Board of Canada and associated publications, 1965–1972. Fish. Res. Board Can. Misc. Spec. Publ. 18: 588 p.

Hachey, H. B. 1965. History of the Fisheries Research Board of Canada. Fish. Res. Board Can. MS Rep. (Biol.) 843: 499 p.

Rigby, M. S., and A. G. Huntsman. 1958. Materials related to the history of the Fisheries Research Board of Canada (formerly the Biological Board of Canada) for the period 1898–1924. Fish. Res. Board Can. MS Rep. (Biol.) 660: 272 p.

LETTERS/LETTRES

Linear Regressions in Fishery Research: Some Comments

PIERRE JOLICOEUR

Département des Sciences biologiques, Université de Montréal, Montréal, Qué.

JOLICOEUR, P. 1975. Linear regressions in fishery research: some comments. J. Fish. Res. Board Can. 32: 1491–1494.

When a statistical relationship has to be described between two variates that are both subject to errors or fluctuations, the *standard major axis*, advocated recently in this journal under the name *GM regression*, is unsuitable. The *ordinary major axis* or, even better, the *bivariate structural relationship*, which includes the ordinary major axis as a special case, should be preferred.

JOLICOEUR, P. 1975. Linear regressions in fishery research: some comments. J. Fish. Res. Board Can. 32: 1491–1494.

Lorsqu'il faut décrire une relation statistique entre deux variables sujettes à des erreurs ou à des fluctuations, *l'axe majeur réduit*, recommandé récemment dans ce périodique sous le nom de *régression GM*, n'est pas convenable. *L'axe majeur ordinaire* ou, encore mieux, *la relation structurale bidimensionnelle*, dont l'axe majeur ordinaire est un cas particulier, sont préférables.

Received May 22, 1974
Accepted May 2, 1975

Reçu le 22 mai 1974
Accepté le 2 mai 1975

IN a recent number of this journal, Ricker (1973) published a review of the utilization of linear regressions in fishery research, with particular reference to situations in which both variates are subject to error of measurement or inherent variability, or both. The present writer has several publications on related topics (Heusner and Jolicoeur 1972; Jolicoeur 1963, 1965, 1968, 1973; Jolicoeur and Heusner 1971; Jolicoeur and Mosimann 1968) and finds himself at odds with several of Ricker's recommendations. In view of the fact that many research workers will tend to rely on Ricker's advice, the readers of this journal should consider the numerous objections that can be raised.

The Standard Major Axis (Ricker's so-called GM Regression)

In situations where what is needed is a description of the statistical relationship between two variates, rather than an estimate of one variate from the other, Ricker advocates using what he calls the *GM regression*, which is nothing else than the *major axis of standardized variates* or, as French workers call it, "*l'axe majeur des variables réduites*" or, for short, "*l'axe majeur réduit.*" In English, incidentally, the simplest and most natural name for this line is the *standard major axis*, rather than *reduced major axis* which Kermack and Haldane (1950) translated literally from the French.

Referring to the slope of the standard major axis (GM regression), Ricker states (1973, p. 413, No. 9) that he has not found any satisfactory statistical treatment supplying the necessary asymmetrical confidence limits, and goes to the length of carrying out a miniature sampling experiment. As discussed several years ago by Jolicoeur and Mosimann (1968), however, an exact (small sample) procedure yielding confidence limits for the slope of the standard major axis has been available for over 30 years, on the basis of the work of Morgan (1939) and Pitman (1939).

But there is a most serious objection against the use of the standard major axis, as indicated by Jolicoeur and Mosimann (1968): the slope of the standard major axis is unsuitable as a parameter of relationship because, when expressed in terms of original (unstandardized) variates X and Y, this slope is equal to the ratio of standard deviations σ_X and σ_Y, and the latter have nothing to do with the presence or the strength of a rela-

Printed in Canada (J3433)
Imprimé au Canada (J3433)

tionship. Ricker himself notes (1973, top of page 413, end of No. 8) that the slope of the GM regression (in his terminology) cannot be used to test association, but he does not appear to realize the full implications of this flaw. Jolicoeur and Mosimann (1968) indicated that, when one has a very large sample, the confidence interval for the slope (σ_Y/σ_X) of the standard major axis becomes extremely narrow even if there is little relationship or no relationship whatsoever ($\rho = 0$)! Contrarily to this, the confidence limits for the slope of the ordinary major axis (of unstandardized variates) discussed by Jolicoeur and Mosimann (1968), Jolicoeur and Heusner (1971), Heusner and Jolicoeur (1972), and Jolicoeur (1973), behave satisfactorily in this respect and can be used for testing significance, just like the confidence limits for the slopes of the usual regression lines of Y on X or X on Y. It is important to remember here that, according to statistical theory, every confidence interval corresponds to a significance test and is derived from that significance test by inversion. The fact that the confidence limits for the slope of the standard major axis cannot be used for testing the significance of a relationship contrasts sharply with what happens in all other regression situations and is symptomatic of a fundamental vice.

Ricker stresses the fact (1973, p. 413, Note 2) that the confidence limits for the slope of the ordinary major axis are much further apart than those for the slope of the standard major axis. Of course, this is not surprising since two different parameters are involved. Moreover, Kermack and Haldane (1950, p. 32) noted many years ago that the slope (σ_Y/σ_X) of the standard major axis could be estimated with a much greater efficiency than the slope of the ordinary major axis. However, Jolicoeur and Mosimann (1968) concluded that this apparently greater efficiency is spurious because it is due precisely to the fact that the slope of the standard major axis is almost insensitive to the presence or strength of a relationship.

Effects of the Units of Measurement (Scaling)

The sensitivity of the slope of the ordinary major axis to changes in the units of measurement, noted by Ricker (1973, p. 415, No. 15), shows that scales of measurement should be chosen carefully. The matter is not simple. It may not even be satisfactory to use the same unit (millimeters) for two measurements of similar nature (linear dimensions of length and breadth, for instance), particularly if there is a marked difference in order of magnitude between the two. Two procedures have been used to cure the sensitivity of the major axis to magnitude and scaling: (1) working with standardized variates, which yields the standard major axis (Ricker's GM regression); however, this procedure is objectionable because the slope of the standard major axis, as already discussed, is unsuitable as a parameter of relationship; (2) transforming data to logarithms; this procedure is often justifiable because positive skewness is very frequent in biological data. As it happens, the logarithmic transformation is frequently beneficial in several respects at once: it tends to cure positive skewness, it tends to straighten out relationships, and, as noted by Jolicoeur (1963) and Jolicoeur and Mosimann (1968), it makes the slope of the ordinary major axis insensitive to changes in the units of original data.

It is surely regrettable that the scale invariance conferred to the slope of the ordinary major axis by the logarithmic transformation does not extend to the case where data are analyzed without transformation. However, a technique that, like the ordinary major axis, is satisfactory in some cases is certainly preferable to a technique that, like the standard major axis, is unsatisfactory in all cases.

It should also be noted that the bivariate structural relationship, a slightly more complex model used by Jolicoeur and Heusner (1971) and which includes the ordinary major axis as a special case, is invariant with respect to scale changes even in the case of untransformed data. All expressions used to estimate the slope of the bivariate structural relationship or to set confidence limits on it are dimensionally homogeneous and have the same dimensionality, in fact, as those for the slopes of ordinary regressions.

Related to the problem of scaling is Ricker's objection that, in the computation of the slope of the ordinary major axis, unlike quantities Σx^2 and Σy^2 (or $s_X{}^2$ and $s_Y{}^2$) are subtracted (Ricker 1973, p. 415, end of No. 15). This objection does not hold; in fact, if Ricker's objection were retained, the standard major axis would fare no better than the ordinary major axis, for it is a particular case of the latter, and the same subtraction occurs implicitly in the definition of the slope of the standard major axis. Finally, Ricker's objection would be entirely irrelevant in the case of the slope of the bivariate structural relationship where Σx^2 (or $s_X{}^2$) is multiplied by the ratio $(\sigma_2{}^2/\sigma_1{}^2)$ of departure variances before being subtracted from Σy^2 (or $s_Y{}^2$), insuring dimensional homogeneity.

Teissier's Alleged "Principle of Least Products"

Following Teissier (1948), Ricker claims that the sum of products of the vertical and horizontal deviations of each point from the fitted line is minimized by the slope of the standard major axis (Ricker 1973, p. 412, No. 8 and p. 415, No. 15). However, this claim does not seem to have been subject to much scrutiny because it can readily be shown that the standard major axis does not minimize the sum of products: it maximizes it! The sum of products of vertical and horizontal deviations from a fitted line can indeed be shown to be

$$(N - 1)[2\, s_{XY} - b\, s_X{}^2 - (1/b)\, s_Y{}^2],$$

where N = sample size,
$s_X{}^2$ = the sample variance of X,
$s_Y{}^2$ = the sample variance of Y,
s_{XY} = the sample covariance of X and Y,
and b = the slope of the fitted line.

While the first derivative of this sum vanishes for $b = \pm(s_Y/s_X)$, the second derivative is negative at $b = +(s_Y/s_X)$ and positive at $b = -(s_Y/s_X)$. Consequently, the sum of products of deviations goes through a (relative) maximum at $b = +(s_Y/s_X)$ and through a (relative) minimum at $b = -(s_Y/s_X)$. Moreover, it is easy to see that this sum does not have an absolute minimum because it decreases to minus infinity when b approaches 0 or ∞ through positive values.

As originally formulated by Teissier (1948, p. 28–29 and as espoused by Ricker, the principle of *least products* is therefore entirely unacceptable. Even if the situation is improved by considering the sum of absolute values of products of deviations, Teissier's contention (1948, p. 29) that the sum of products is maximum at $-s_Y/s_X$ is still erroneous: the sum of absolute values of products of vertical and horizontal deviations goes through a relative minimum at $-s_Y/s_X$ as well as at $+s_Y/s_X$. Considering the rather queer behavior of the sum of products in addition to the fact that, after more than 25 years, Teissier's alleged principle of least products has not been found valid or useful in statistical contexts, any attempt to base a statistical procedure on this dubious criterion appears certainly ill-advised.

The Ordinary Major Axis and the Bivariate Structural Relationship

In contrast with the standard major axis (Ricker's GM regression), the validity of the bivariate structural relationship and of its kindred the ordinary major axis is well demonstrated in statistical literature, provided one recognizes that biological variation is hardly ever homogeneous and that multiple factors and levels of variation are the rule rather than the exception in biology. From a statistical viewpoint, it is irrelevant whether departures from a trend are due to genuine biological fluctuations or to errors of measurement, as long as both are distributed and sampled in the same way. According to the current statistical consensus (Kendall and Stuart 1961; Moran 1971; Sprent 1969), the variation responsible for a trend is defined to be random in the case of a *structural relationship* and systematic in the case of a *functional relationship*; in the bivariate normal case, the estimates of the slope of the ordinary major axis and of the slope of the structural relationship are known to satisfy not merely the criterion of least squares but also the principle of maximum likelihood (Moran 1971). The confidence limits for the slope of the ordinary major axis (and of the bivariate structural relationship) are sometimes imaginary, as noted by Ricker (1973, page 413, Note 2), but it has been shown recently in an extensive sampling experiment (Jolicoeur 1973) that imaginary confidence limits occur only when correlation is not significant and do not create problems, neither in theory nor in practice.

In a recent analysis of metabolic data, Jolicoeur and Heusner (1971) decided to use the *bivariate structural relationship* because, in their opinion, the major axis would have implied an overly simple model of the observed biological variation and an unduly precise assumption. According to the major axis model (ordinary or standard), all variation is interpreted in terms of only two underlying (unobserved) variates: the coordinate along the major axis, representing the trend, and the coordinate along the minor axis, representing departures from the trend. This interpretation of departures from a trend in terms of a single underlying variate is generally unrealistic in biology, even in the case of natural variation, because it implies that the deviations of the two observed variates from the trend would be rigidly related to each other: if, for instance, a rat departs from a metabolic trend in having a higher standard oxygen consumption, it would necessarily depart from that trend too in having a lower weight. Seasoned research workers know that physiological and ecological processes are practically never that simple. Fortunately, the *bivariate structural relationship* model is only slightly more complex than the major axis, yet it allows for the interpretation of deviations from a trend in terms of independent underlying variates, one for each observed variate: thus some rats may develop a tendency to obesity without showing the corresponding increase in standard metabolism, while others may have an exceptionally high metabolism without necessarily losing weight. The possibility of independent departures from a trend, provided by the bivariate structural relationship, is certainly a closer approximation to biological reality. While the necessity to make assumptions about the ratio λ of departure variances may seem uncomfortable at first to some workers, one should remember that the principal purpose of statistical methods is not to make scientists feel comfortable: it is to help investigators to obtain correct information from data. A statistical procedure like the bivariate structural relationship, where assumptions and the limitations of conclusions are explicit, is certainly safer in this respect than procedures where assumptions and limitations remain implicit.

HEUSNER, A. A., AND P. JOLICOEUR. 1972. Allometry of the standard oxygen consumption in the white rat, p. 22–24. *In* Proc. Int. Symp. Envir. Physiol. (Bioenergetics), Dublin, 1971. FASEB, Bethesda, Maryland.

JOLICOEUR, P. 1963. The multivariate generalization of the allometry equation. Biometrics 19: 497–499.

1965. Calcul d'un intervalle de confiance pour la pente de l'axe majeur de la distribution normale de deux variables. Biom.-Praxim. 6: 31–35.

1968. Interval estimation of the slope of the major axis of a bivariate normal distribution in the case of a small sample. Biometrics 24: 679–682.

1973. Imaginary confidence limits of the slope of the major axis of a bivariate normal distribution: a sampling experiment. J. Am. Stat. Assoc. 68: 866–871.

JOLICOEUR, P., AND A. A. HEUSNER. 1971. The allometry equation in the analysis of the standard oxygen consumption and body weight of the white rat. Biometrics 27: 841–855.

JOLICOEUR, P., AND J. E. MOSIMANN. 1968. Intervalles de confiance pour la pente de l'axe majeur d'une distribution normale bidimensionnelle. Biom.-Praxim. 9: 121–140.

KENDALL, M. G., AND A. STUART. 1961. Functional and structural relationship, Chapter 29. *In* The advanced theory of statistics, Vol. 2. Griffin and Co. Ltd., London.

KERMACK, K. A., AND J. B. S. HALDANE. 1950. Organic correlation and allometry. Biometrika 37: 30–41.

MORAN, P. A. P. 1971. Estimating structural and functional relationships. J. Multivar. Anal. 1: 232–255.

MORGAN, W. A. 1939. A test for the significance of the difference between the two variances in a sample from a normal bivariate population. Biometrika 31: 13–19.

PITMAN, E. J. G. 1939. A note on normal correlation. Biometrika 31: 9–12.

RICKER, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

SPRENT, P. 1969. Models in regression and related topics. Methuen and Co. Ltd., London. 173 p.

TEISSIER, G. 1948. La relation d'allométrie: sa signification statistique et biologique. Biometrics 4: 14–48.

A Note Concerning Professor Jolicoeur's Comments

W. E. RICKER

3052 Hammond Bay Rd., Nanaimo, B.C.

RICKER, W. E. 1975. A note concerning Professor Jolicoeur's comments. J. Fish. Res. Board Can. 32: 1494–1498.

The ordinary major axis of a bivariate normal distribution is unsuitable for describing the functional relationship (in Lindley's general sense) between two naturally variable quantities, because it is not invariant with scale and because qualitatively unlike quantities are subtracted in computing it. The bivariate structural relationship is unsuitable because one of the parameters required, λ, cannot be estimated from naturally variable data; in fact λ has no objective meaning for such data. The standard major axis (or GM regression line) has neither of these defects, and it is the line that minimizes the sum of products of the absolute vertical and horizontal deviations of data points from itself.

RICKER, W. E. 1975. A note concerning Professor Jolicoeur's comments. J. Fish. Res. Board Can. 32: 1494–1498.

L'axe majeur ordinaire d'une distribution normale bidimensionnelle ne convient pas pour décrire la relation fonctionnelle (dans le sens général que lui donne Lindley) entre deux quantités

Printed in Canada (J3493)
Imprimé au Canada (J3493)

naturellement variables, parce qu'il n'est pas invariable par rapport à l'échelle et que des quantités qui diffèrent qualitativement sont soustraites lors des calculs. La relation structurale bidimensionnelle n'est pas convenable, parce que l'un des paramètres requis, λ, ne peut être estimé à partir de données naturellement variables; en fait, λ n'a pas de signification objective pour de telles données. L'axe majeur réduit (ou régression GM) ne possède aucun de ces défauts, et est la ligne qui minimise la somme des produits des déviations verticales et horizontales absolues des points découlant des données par rapport à l'axe lui-même.

Received July 15, 1974
Accepted May 2, 1975

Reçu le 15 juillet 1974
Accepté le 2 mai 1975

1. Professor Jolicoeur calls attention to an important omission from my 1973 paper, namely that I had not discovered already existing formulae for confidence limits of the GM regression. Jolicoeur and Mosimann (1968) quote these as expressions (31) and (32) on page 133 of their paper. They are:

$$v(\sqrt{B+1} - \sqrt{B}) \text{ and } v(\sqrt{B+1} + \sqrt{B}) \quad (1)$$

$B = F(1 - r^2)/(N - 2)$
v = GM regression of Y on X, or standard major axis
r = correlation coefficient between Y and X
N = number of pairs of variates
F = the variance ratio at the desired confidence level for $n_1 = 1$ and $n_2 = N - 2$ degrees of freedom (to be obtained from an F table, available in most statistical textbooks).

For the example of figure 2 of Ricker (1973) the above limits are 0.59 and 1.66 for N = 11, and 0.71 and 1.38 for N = 25. These asymmetrical limits obviously agree with the two empirical distributions better than do the approximate symmetrical limits drawn on that figure.

2. The other matter raised by Professor Jolicoeur concerns the relative suitability of the ordinary major axis and the standard major axis to describe the central trend or functional regression (in the general sense) of a bivariate normal distribution, in the case where essentially all of the variation is natural rather than the result of errors of measurement. Both statistics are being used for this purpose in the statistical literature. It should be possible to demonstrate that one of them is always superior to the other, or else to define separate fields of usefulness for each. Professor Jolicoeur's position appears to be that the ordinary major axis is usually suitable when both the variates are in logarithms, and that the standard major axis should be avoided for all types of data. My contention, following Jones (1937) and Moran (1972), is that the standard major axis is always suitable for naturally variable data, whether in terms of logarithms or not, and that the ordinary major axis is appropriate only if it happens to coincide with the standard one.

The name major axis stems from the fact that when a bivariate normal array of observations is plotted, the points will occupy an elliptical field whose major axis is the "ordinary" major axis referred to above. Actually a whole series of ellipses can be calculated about any major axis, which (within limits of sampling error) will enclose any desired percentage of the observed points, for example 90%, 95%, or 99%. Figure 1 shows an example of such an ellipse and its major axis (AM). Also shown are the corresponding standard major axis (AMR) and the two ordinary regression lines (R and R′), as well as the geometrical relationships among these statistics. However, in order for the major and minor axes of the ellipse to be at right angles on a graph such as Fig. 1, it is essential that a unit of measurement be of the same absolute length on each coordinate axis. If this is not so, the major and minor axes of the ellipse meet at an oblique angle, although both they and the ellipse itself have exactly the same position as previously relative to the observations; and what is more confusing, the major axis no longer *appears* to be the central trend line of the ellipse, because the eye tends to interpret the distribution of the points in terms of equal scales.

3. Consider then the ordinary major axis. Its formula is:

$$\frac{\Sigma y^2 - \Sigma x^2 + [(\Sigma x^2 - \Sigma y^2)^2 + 4(\Sigma xy)^2]^{\frac{1}{2}}}{2\,\Sigma xy} \quad (2)$$

This expression was developed in the last century. If X and Y represent distances on a plane at right angles to each other, and x and y are the same distances measured from their means, then expression (2) defines the slope of the line that minimizes the sum of squares of the distances from the observed points to the line, measured at right angles to the line.

However, we are interested not in pure geometry but in observed quantities, and once X

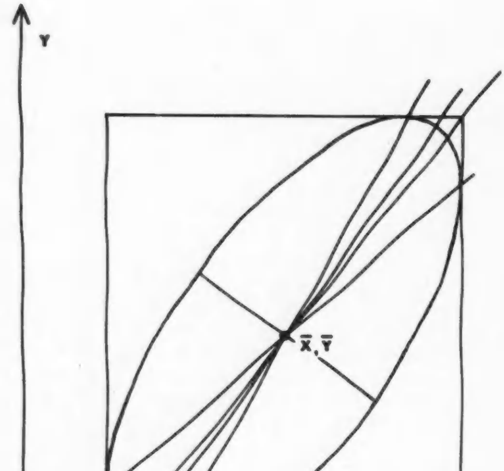


FIG. 1. The relationships between the ordinary regression lines (R and R'), the correlation ellipse, its major axis (AM), and the standard major axis or GM regression (AMR), when one unit of measurement occupies the same distance on the X and Y axes. If the unit used to measure X or Y is changed, the positions of R, R', and AMR remain unchanged relative to the observed points, but AM shifts to a new position somewhere between R and R'. (From figure 1 of Mayrat 1970, with the minor axis of the ellipse added.)

and Y are measured in physical units, trouble arises. In expression (2), Y might be the number of fish per hectare in a body of water, and X the animal plankton in grams per cubic meter: how then can x^2 be subtracted from y^2? To do so violates a fundamental principle of applied mathematics. Even if converted to logarithms, Y and X are still incommensurable. Expression (4) below shows that to get around this difficulty it is necessary to introduce at three points in (2) a factor λ whose dimensions are Y^2/X^2. However, this requires information that is not available from naturally variable data.

Another characteristic of the major axis is that its slope changes if the units of measurement are changed. In Fig. 1, for example, if the unit used for the Y variates were to be changed from centimeters to millimeters, and 1 mm is given the same space as 1 cm had formerly, the array of points and the ellipse become 10 times as long vertically. At the same time the slope of its major axis increases somewhat *more* than 10 times, as can be verified by computation from expression (2). Thus, the major axis is not invariant with scale; for each set of units there is a different major axis for an ellipse that always has the same position relative to the observed data. And since there is an indefinitely large number of major axes, we must discover whether one of them has some unique and desirable properties.

Professor Jolicoeur points out that when data are in terms of logarithms, a change in the original units used (not the logarithms) will not change the position of the ordinary major axis. But while this meets the criterion of uniqueness, it fails to meet the objection that unlike things are subtracted in computing it, and in any event it applies to only one class of data.

4. Consider now the GM regression or standard major axis. Its formula is simple; in terms of x and y it is equal to:

$$\sqrt{\Sigma y^2/\Sigma x^2} \qquad (3)$$

It is also the ratio of the standard deviation of Y to the standard deviation of X; and as its name implies, it is the geometrical mean of the regression of Y on X and the reciprocal of the regression of X on Y (the reciprocal is used in order to refer both regressions to the same coordinates). The dimensions of the GM regression are Y/X, as is necessary for any regression of Y on X. Teissier (1948) showed that the line described by (3) is that which minimizes the sum of the products of the horizontal and vertical deviations of the observed points from itself.[1] Hence it is analogous to a least squares line, but one made symmetrical with respect to Y and X. On this basis it stands on its own feet; it is independent of any derivation from more complex relationships, and there is no subtraction of quantities that are qualitatively different, either implicit or overt.

---

[1] Professor Jolicoeur calls this "Teissier's principle of least products," and says that it produces a maximum rather than a minimum. This is true for products derived from the formula on p. 1493 of his Comments, provided the standard major axis is positive. It results from the fact that the formula takes the signs of the deviations into account: for positive b their products are all negative, and the formula gives a negative sum which is a maximum when $b = s_Y/s_X$ because on either side of it lie numerically larger negative values. For negative b the products of the deviations are all positive, and differentiation of the formula shows that their sum is a *minimum* when $b = -s_Y/s_X$. However, for establishing the position of a line of best fit the signs of the deviations are of no concern; they should all be considered as of the same sign, and on this basis Teissier's principle is correct for both positive and negative values of the standard major axis.

The standard major axis always occupies the same position relative to the observations, whether these are in logarithms or not. In Fig. 1 this means that the numerical value of the slope AMR will vary strictly in proportion to any change in units. In that respect it is unique among all possible major axes lying between R and R′. Furthermore, it is easy to make the ordinary major axis coincide with the standard major axis without any loss of generality in either. It is only necessary to adjust the scales of the X and Y axes so they are in terms of their respective standard deviations, or bear the same ratio to them. When this is done the variances of Y and of X are the same, and expressions (2) and (3) are both equal to 1.

What then about Professor Jolicoeur's "most serious objection" to the standard major axis (or GM regression), that "this slope is equal to the ratio of the standard deviations σ_X and σ_Y, and the latter have nothing to do with the presence or the strength of a relationship"? It is true that the ratio of σ_X to σ_Y is not related to the presence or strength of a relationship, but the GM regression should not and need not be used to measure that strength. For that purpose the correlation coefficient (r) provides a test that is perfectly adequate, and one that is symmetrical with respect to the variates X and Y. Nothing more is needed. The function of the GM regression is solely to provide a line of best fit. As Professor Jolicoeur points out, with large numbers of variates the position of the GM regression can be established within narrow limits of confidence even when r is quite small. This is an advantage, not a disadvantage; and it is completely irrelevant whether the limits of error of the GM regression are narrower or wider than those of the standard major axis.[2]

5. Consider finally the "general structural relationship." This belongs to the fourth or "error-in-variables" model of Moran's (1971) fourfold classification of regressions. That is, it was developed with reference to data in which all the variability about a regression line is a result of errors of measurement. In that situation deviations of observed points from the true relationship are the resultant of two components, the variance of Y when X is fixed without error, and the variance of X when Y is fixed. In principle certainly, and sometimes also in practice, these two "point" variances can be estimated, although it requires extra information, additional to what is in an ordinary set of pairs of variates. The ratio of the point variances is represented by λ, and the slope of the structural relationship is:

$$\frac{\Sigma y^2 - \lambda\Sigma x^2 + [(\lambda\Sigma x^2 - \Sigma y^2)^2 + 4\lambda(\Sigma xy)^2]^{\frac{1}{2}}}{2\,\Sigma xy} \qquad (4)$$

The problem is, should the concept of point variances, and hence expression (4), be applied also to data in which all the variability is natural? Such data belong in Moran's second or "correlation" model, in which errors of measurement have no place. Two examples will illustrate why the general structural relationship is not applicable to them. The first situation is represented by an example of Teissier (1948) and by the first two examples of Jolicoeur and Mosimann (1968), in which it seems clear that no division of variances can be made or even imagined. For example, in relating the length (l) and breadth (w) of the carapace of turtles of a given species, it is obvious that if a carapace becomes relatively longer it is automatically relatively narrower. There is no way to separate the two effects, or to decide whether l or w makes the greater contribution to observed deviations from the trend of log w plotted against log l. We must therefore follow Teissier's lead and use the GM regression, which gives each dimension equal weight by minimizing the sum of products of the observed absolute log deviations in the vertical and horizontal directions.

What about the more usual situation where the variates being compared have no such reciprocal relationship? Consider, for example, the relation between basal metabolism and weight in adult rats, as studied by Jolicoeur and Heusner (1971). Here too no logical or biological basis emerges for considering that observed deviations can be partitioned into two components, one due to variations in metabolism and another due to variations in weight. Jolicoeur and Heusner discuss the problem of estimating the necessary point variances, and conclude that it is impossible to obtain the required information. One reason for the difficulty is that they were searching for something that has no objective reality. It is true that a series of metabolisms might be taken from a single rat of constant weight, but they point out that rats of a given weight may vary in fatness and in the relative size of their internal organs, both of which must in turn affect metabolism, so that such a series would not necessarily be representative. And to get a series of weights corresponding to a fixed metabolism defeats the imagination, because any observed metabolism will include the effect of its own variability. More fundamentally, a rat's endocrine balance and many other physiological, psychological, and environmental characteristics can affect both weight and metabolism, so that the relation between the latter must be the result of a great complex of effects and interactions. That one aspect of this complex should remain unchanging while another varies seems impossible, not only in practice but also in principle, and hence the ratio λ cannot be estimated because it does not exist.

---

[2] Nevertheless, it is true that even when the ordinary major axis and the standard major axis coincide and both are equal to 1, the formulae given by Jolicoeur and Mosimann (1968) indicate wider confidence limits for the former than for the latter.

Comparable considerations apply to other examples of natural variability. For those who are not convinced, I feel that the onus lies with them to demonstrate that the concept of component point variances and the use of the ratio λ is actually applicable in each individual situation. Failing this, we must accept the simpler idea that *natural* variability from a trend line is one and indivisible, and hence use the GM regression to estimate the position of that trend. This removes the necessity for making unsatisfactory guesses about possible values of λ, and provides a slope that is a unique best estimate of the statistic desired.

6. In conclusion, recently I discovered by accident that the GM regression was used as early as 1916 in a meteorological paper by H. Sverdrup. It may be that many others have arrived at the same expression by intuition, for it seems very natural to employ the geometric mean of the two ordinary regressions as a measure of central trend. But this of course does *not* apply to the variability due to errors of measurement, except in the special case where $\lambda = \Sigma y^2/\Sigma x^2$ and expression (4) reduces to (3).

7. Mr F. W. Nash of the Computer Centre of the Nanaimo Biological Station has been of great assistance with respect to the mathematical and geometrical aspects of the various axes.

(In addition to those cited in Professor Jolicoeur's comments.)

JONES, H. E. 1937. Some geometrical considerations in the general theory of fitting lines and planes. Metron 13: 21–30.

MAYRAT, A. 1970. Allométrie et taxonomie. Rev. Statist. Appliquée 18: 47–58.

SVERDRUP, H. 1916. Druckgradient, Wind und Reibung an der Erdoberfläche. Ann. Hydrogr. u. Maritimen Meteorol. (Berlin) 44: 413–427.

BOOK REVIEWS/COMPTES RENDUS

Color Atlas of the Diseases of Fishes, Amphibians and Reptiles. *By E. Elkan and H. Reichenbach-Klinke (Marsha Landolt [ed.]) T. F. H. Publications Inc., Neptune, N.J. 1974. 256 p. $30.00.*

This book is a companion to the authors' "Principal Diseases of Lower Vertebrates" published in 1965 and to the three later American volumes (T.F.H. Publications Inc. Ltd.). It is intended to assist the amateur diagnostician in determining the cause of common diseases of fishes, amphibians, and reptiles by providing for his perusal a large number of presumably "new" color photographs (macro and micro) of typical cases of disease. The atlas is divided into seven sections; Viral Diseases (20 plates), Bacterial Diseases (52 plates), Parasitic Diseases (224 plates), Genetic Disorders and Trauma (9 plates), Nutritional Disorders (21 plates), Environmental and Hematological Diseases (12 plates), and Neoplastic Diseases (47 plates). The section on parasitic diseases is obviously the largest and includes such diverse groups as fungi, protozoans, worms, leeches, copepods, and insects. The book has no text and about 5% of all the figures are not in color.

The main criticisms I have of this book are that it is not usefully organized and documented, and that a high proportion of the photographs have already been published in color, mostly by T.F.H. Publications. Some photographs have, indeed, appeared in color in every T.F.H. volume dealing with fish diseases. While this is no crime, it diminishes the chief raison d'être of this atlas which appeared to be this first opportunity to publish an accumulated series of useful color photographs, an event previously not economically feasible. The organization of the photographs is such that one would already have to know in general the causative agent of a disease in order to use the book efficiently. It is, furthermore, questionable if a person interested in fish diseases, for example, would desire or utilize photographs of amphibian and reptilian diseases or disease agents scattered throughout the book.

Although, as the authors indicate, many of the lower vertebrates may show no external signs of disease prior to death, the organization of the photographs could more effectively have paralleled a sensible, systematic, gross examination of the specimen like that described so thoroughly by Reichenbach-Klinke in his "Fish Pathology" (T.F.H. Publication PS-204). Photomicrographs could have been grouped with photographs of the gross lesions and then cross-indexed by host, agent, tissue and organ. Such a system would have distinguished a diagnostic guide from a mere photograph album.

The authors feel that publication of even an unsystematically collected group of photographs has value, and while this is doubtless true, it is disappointing to find that these experienced workers have apparently not yet implemented a complete system of pathologic documentation, especially to include relevant "normals" along with the abnormals.

It is regrettable that most of the captions lack useful information such as magnification, stain used and salient features of case history, e.g. age, sex, source of the specimen and whether from fresh, salt, or brackish waters. Photomicrographs in particular would often have benefited from indicators pointing to critical details. A few examples might help to illustrate some of my criticisms and reasons for disappointment. Figures 27 and 31 are murky and the captions fail to mention culture media and the age of the culture. Figures 69, 156, 166, 187, 251, 252, 300, and 312 are badly out of focus. Many photomicrographs are poorly illuminated and show marked curvature of field: Fig. 57, 85, 129, 262, and 287, 294, 347, 363, 366, respectively. Incidentally, what is a photograph (Fig. 267) of a "worm which parasitizes crayfish" doing in this book?

Some readers would take issue with the authors for putting UDN (ulcerative dermal necrosis) in the section on environmental diseases without qualifications, and many readers would take issue with calling *Dermocystidium* both harmless and a microsporidian. A few of the ubiquitous photographs are inconsistently captioned, e.g. Fig. 170 indicates *Henneguya* from pike but in Reichenbach-Klinke's Fish Pathology (T.F.H. Publications) *Henneguya* from carp (p. 87); Fig. 105 Trypanosoma from a European eel but in Fish Pathology the specimen is said to be from an American eel (p. 141), and finally, Fig. 232 refers to *Triaenophorus crassus* but the same photograph is *T. nodulosus* on p. 116 of Hoffman and Meyer (Parasites of Freshwater Fishes, T.F.H. Publications). Perhaps these apparent inconsistencies are merely corrections of earlier mistakes.

It is easy to be critical of others' work but difficult to be creative, and I for one would like to express my gratitude to the authors for their fine contributions in the past to fish pathology. However, in my opinion the cost:benefit ratio of their latest book would be too high for most prospective buyers.

GORDON R. BELL

Department of the Environment
Fisheries and Marine Service
Pacific Biological Station
Nanaimo, B.C. V9R 5K6

(R48)

Fisheries of the North Pacific. *By Robert J. Browning. Alaska Northwest Publishing Company, Anchorage, Alaska. 1974. 408 p. $24.95.*

"It is intended as a guide to the history of the fisheries, the biology of the species, the vessels of the fisheries, assembly of gear, fishing methods, the handling of the catch at sea and ashore, and processing of fishery products. There is also an attempt at assessment of the future of these fisheries..." Page VI.

It is that and more; it is 408 large sized pages of readable, authoritative, and well-illustrated information on these topics in the area from California to the Bering Sea. It includes, along with descriptions of many others, the fisheries for oysters, clams, barracuda, carp, Pacific sardine, pomfret, salmon, halibut, king crab, and dungeness crab. It includes, among others, descriptions of halibut schooners, Alaska limit boats, troll boats, and seine boats. It includes descriptions plus construction and operating details of trawls, seines, longlines, troll gear, pots, and fish wheels. It includes three chapters largely in nontechnical language on fish handling and preservation at sea and ashore.

The amount of detail in most chapters is enormous and is indicative of the efforts of the author to dig to the bottom of every topic. To use halibut as an example, one finds included descriptions of the spawning process, history of the early fishery, development of international agreements, evolution of the halibut schooners, construction details of the longline gear used for halibut, proper handling of fish, use of ice for preservation, and procedures for freezing.

Most of the book is a compendium from many other authors but the sections on fishing vessels and fishing gear are largely original with the author or his collaborators. These chapters that comprise about 40% of the book are a fascinating mixture of history, methods of operation, and construction details, complete with many illustrations.

The author is an ex-newspaper reporter who has been a commercial fisherman and who loves fishing, fishermen, fishing vessels, and the northeast Pacific ocean. The result is a book for fishermen or fishery scientists or anyone else who shares that love and wants to know more about any aspect of these fisheries.

WILLIAM F. ROYCE
National Marine Fisheries Service,
NOAA,
Washington, D.C. 20235, USA

(R4)

Algal Physiology and Biochemistry *(Botanical Monographs Vol. 10). Edited by W. D. P. Stewart. University of California Press, Berkeley and Los Angeles. 1974. ix, 989 p. $40.00.*

As implied by the Editor in his preface, this book attempts to cover in one "fat" volume an up-to-date (in fact up to middle of 1972) picture of various (but not all) aspects of algal physiology and biochemistry. Although rather arbitrarily chosen, the topics cover a vast, but well-balanced, range of scientific interests, with the potential to attract students, teachers, and researchers involved in the fields of phycology, plant physiology, and biochemistry, as well as limnology and oceanography. Each topic has been accorded a fairly comprehensive coverage by one or more distinguished contributors (32 topics, 35 contributors), and this coverage has tended to concentrate on the eukaryotic algae with minimal treatment of the prokaryotic blue-green algae; the Editor's apology for this discrimination is justified by the recent publication of two monographs covering virtually all conceivable aspects of the science of blue-green algae (see Carr and Whitton 1973; Fogg et al. 1973).

As may be expected from the "strait-jacket" space limitations imposed on the contributors by an editor committed to producing a gigantic monograph, several chapters suffer from being packed with so much detail as to make them excessively "heavy" for the younger inexperienced reader. I would not be surprised to find students in particular being "turned off" by such chapters. On the other hand, many chapters (e.g. biochemical taxonomy, plastids, chlorophylls, storage products, CO_2-fixation, photoreduction-anaerobic growth, photorespiration, heterotrophy, nitrogen assimilation, silicification–calcification, vitamins-growth regulators, morphogenesis, extracellular products, movements, etc.) make stimulating and enjoyable reading, apart from comprehensively reviewing their respective areas. It is interesting that a monograph devoted to physiology and biochemistry has nevertheless included two excellent chapters on algal cytology (such as cytoplasmic organelles and plastids), that serve to provide the appropriate "organismic" background for the chemical and biochemical insights gleaned from the other chapters.

As may be expected from the immense size of this monograph, some errors of detail are inevitable but I am inclined to think that many of these errors can be rather misleading not only to the inexperienced student but also for the specialist seeking information outside his specialty. It appears that the individual contributors have not sufficiently cross-checked related chapters by other contributors in the same monograph. Govindjee and Braun (p. 354) quote lutein as the major xanthophyll of red algae, Lewin (p. 5) and Goodwin (p. 183) attach equal importance to lutein and zeaxanthin, while Bisalputra (p. 153) considers zeaxanthin as the predominant xanthophyll in this algal class. Goodwin (p. 183, 187) has correctly pointed out that the major xanthophyll of Xanthophyceae and Euglenophyceae is the acetylenic epoxide *diadinoxanthin* and not the ethylenic epoxide *antheraxanthin* as was previously believed, which revision is recognized by Bisalputra (p. 153, 154) but overlooked by Lewin (p. 5) in the case of Euglenophyceae. It is quite disturbing to read on p. 4 of Lewin's chapter on biochemical taxonomy that lutein is the principal xanthophyll of Euglenophyceae and to find in the pigment-distribution Table facing this page that lutein is omitted from this algal class; fortunately, both Bisalputra (p. 154) and Goodwin (p. 187) have correctly excluded lutein from the carotenoid composition of euglenoids (however, Goodwin's placement of zeaxanthin in this algal class is dubious). It should also be pointed out that Bisalputra (p. 154) is incorrect in including chlorophyll *c*, diatoxanthin, and heteroxanthin among the pigments of Eustigmatophyceae. I suggest that Govindjee and Braun (p. 361) are not serious when they state without any authentication that the Cryptophyceae contain lutein; here is a glaring case of lack of communication with the other contributors such as Bisalputra (p. 154) and Goodwin (p. 187) who have correctly listed the unique carotenoid composition of this class of algae. These are examples of information errors or inconsistencies that I have detected in the course of rapid perusal of topics with which I am most familiar. Keeping in mind the probability of similar errors and oversight in the other chapters, I caution the inexperienced student and elementary-course teacher to treat this monograph not as an encyclopedia of "hard-core" facts but rather as a handy summation of recent thinking and ideas in the relevant areas of phycology and plant physiology.

The book is well printed with some beautiful and other appropriate illustrations, but then the purchaser does expect these qualities in return for its high price.

CARR, N. G., AND B. A. WHITTON. 1973. The biology of blue-green algae. Bot. Monogr. Univ. of California Press, Berkeley, Calif. 9: 676 p.

FOGG, G. E., W. D. P. STEWART, P. FAY, AND A. E. WALSBY. 1973. The blue-green algae. Academic Press Inc., London and New York, 459 p.

NAVAL J. ANTIA

Department of the Environment
Fisheries and Marine Service
Pacific Environment Institute
West Vancouver, B.C. V7V 1N6

(R58)

Pollution Ecology of Freshwater Invertebrates.

C. W. Hart Jr. and Samuel L. H. Fuller [ed.]. Academic Press Inc., New York and London. 1974. 389 p.

This book contains 10 chapters, each from a different pen and each dealing with one group of invertebrates that has been the subject of special study by the author or authors of the chapter. As the editors point out, coverage is far from complete; for instance, only crayfish feature among the crustaceans, and the treatment is varied. The accounts also tend to be rather narrowly North American and thus they somewhat belie the title.

Some of the chapters, for instance those on the protozoans and the insects, contain much tabulated data showing ranges of chemical parameters in which particular species have been collected, or lethal and tolerated concentrations of various toxins in the laboratory. The first of these approaches is not very useful, as is pointed out in Willard Harman's much superior chapter on snails, because it largely reflects the range of conditions studied by the collector. And the second approach, as it has been applied to the Protozoa, almost totally ignores the extensive and excellent work of various Europeans on this subject. Only one reference to Hartmut Bick's large volume of good work is given and that is in badly mutilated German; Vladimir Sladeček is not even mentioned. Here was the one place in the book where *all* the overseas work would have been directly relevant and practically no account is taken of it. In my opinion neither of these two chapters is very useful.

On the other hand, the one on oligochaetes would lead the pollutional novice very well into the literature and our general concepts on the effects of pollution on Tubificidae and Naididae, and several of the other chapters contain valuable accounts of what is known about the ecology of other groups. These are sponges, triclads, leeches, bryozoans, crayfish, bivalves, and snails. In most of these, the reader is given a good modern account of the North American taxonomy, with an ample bibliography, a general account of the ecological biology of the group, and an attempt at an assessment of the effects of pollution, and other human activity, upon it.

In the last part the treatment is, like our knowledge of the topic, often scrappy and indecisive, but the authors have struggled manfully with their tasks and gathered facts, opinions, guesses, and fantasies from the literature. Some, such as John Bushnell, even did experiments for the purpose of his chapter on bryozoans.

Scattered through the book there is much useful ecological information on, for instance, the effects of silt on sponges, how to name epigean triclads, the prey of each leech species, the resistance of ectoprocts to poisons, the fish hosts of unionaceans, and the uses of diversity indices. These are the valuable features of a book that set out to achieve an impossible task, and failed.

The reader can learn a great deal about some groups of (North American) freshwater invertebrates from it, but the novice who expects to find out all about pollution because of the title will find only confusion. However, as this is the state of the art perhaps that is fair enough. The protozoan and insect chapters would have been very much better had they been less narrowly parochial, and they are probably best ignored, but the other chapters are worth reading even by non-North Americans. Not all the authors are unaware of the rest of the world and many of their accounts are excellent.

H. B. N. HYNES

Department of Biology
University of Waterloo
Waterloo, Ont. N2L 3G1

(R56)

Books Received/Livres reçus

March–April 1975

***Ageing of Fish.** *Proceedings of an International Symposium. Edited by T. B. Bagenal. Unwin Brothers Limited, The Gresham Press, Surrey, England, 1974. vi + 234 p. £5.00, U.S. $16.*
(Twenty-one papers on physiological processes leading to formation of otoliths, scales, and fin rays, as well as methods of age determination and source of errors.)

***The Benthos of Lakes.** *R. O. Brinkhurst. MacMillan of Canada Limited, Toronto, 1974. xii + 190 p. £14.00, $45.95 Canadian.*
(Discussion of classical and modern concepts in study of benthos in lakes, together with author's own views.)

Collecting Marine Tropicals. *Rodney Jonklaas. T.F.H. Publications, Inc., Neptune City, N.J., 1975. 224 p. $17.50.*
(Collecting methods and gear for wading and scuba diving collectors, including many color illustrations of tropical fishes.)

***Culture of Bivalve Molluscs. 50 years' experience at Conwy.** *P. R. Walne. Fishing News (Books) Limited, Surrey, England, 1974. 173 p. £5.85 (about $14.00 Canadian).*
(Summary of 50 years research into culture of oysters and other bivalves at the Fisheries Experiment Station at Conwy, Wales.)

Fish Pathology. *Heinz-Hermann Reichenbach-Klinke in collaboration with Marsha Landolt. T.F.H. Publications Inc., Neptune City, N.J., 1973. 512 p. $20.00.*
(Lavishly illustrated guide to recognition and treatment of diseases and injuries of fishes, with emphasis on environmental and pollution problems.)

***Fisheries and Energy Production.** *A Symposium. Edited by Saul B. Saila. D. C. Heath and Company, Lexington, MA., 1975. viii + 300 p.*
(Twelve articles presenting a balanced report on U.S. electrical energy supply and the effort to minimize potential environmental damage to surrounding aquatic life.)

***Light's Manual. Intertidal Invertebrates of the Central California Coast.** *Third Edition. Edited by Ralph I. Smith and James T. Carlton. University of California Press, Berkeley, 1975. xviii + 716 p. $20.00.*
(Keys to the intertidal invertebrates from the Monterey Peninsula to Bodega Head, with brief treatment of biology of major taxa, collection and preservation methods, annotated systematic lists, and selected references also provided.)

***Population and Community Ecology: Principles and Methods.** *E. C. Pielou. Gordon and Breach, New York, N.Y., 1974. viii + 424 p. $39.00.*
(Text for two-semester, undergraduate course.)

The Work of the River. *C. H. Crickmay. MacMillan of Canada Limited, Toronto, 1974. xvi + 271 p. £12.00 (about $28.80 Canadian).*
(Role of fluvial processes in shaping the landscape.)

---

*Book to be reviewed.

OBITUARY

Albert Lewis Tester

1908-1974

Dr Albert Lewis Tester died in Honolulu, Hawaii, on November 27, 1974, his 66th birthday.

Al Tester was a man of many parts. He gained an international reputation for his research on herring and sharks. He was a first-rate lecturer and interpreter of science to professional and layman. His university courses were models of organization and clarity. He was a reluctant but able administrator. Countless people have been influenced in some way by Al Tester, not least, perhaps, by the integrity and thoroughness of his approach to everything he did.

Al was born in Toronto and educated at the University of Toronto, where he received his Ph.D. in 1936. In 1931 he went to the Pacific Biological Station of the Biological Board of Canada (later the Fisheries Research Board of Canada) at Nanaimo, B.C., to study Pacific herring. Thus began a highly productive period of herring research that lasted 17 years. Al noted large annual fluctuations in catches in the various areas of the coast and he speculated that these reflected fluctuations in abundance. The question was whether there was a single homogeneous stock that moved erratically along the coast or whether there were several discrete stocks, any one of which might be seriously depleted by overfishing. Tester's extensive morphometric studies and tagging and recovery programs showed that the stocks were more or less distinct with intermingling decreasing with distance. These classic studies led him to recommend catch quotas for individual stocks, a system of management that has continued to the present.

On the basis of coast-wide age determinations and spawning assessment, Al estimated recruitment in the various stocks and issued remarkably accurate annual predictions on abundance for the guidance of the fishing industry. He also pioneered the assessment of the size of herring schools on local fishing grounds by echo sounder, which proved useful in determining whether catch quota extensions could be recommended.

In the mid-40s Al developed a lifelong interest in the intricacies of population dynamics and biometry, spending a period at the Institute of Statistics, North Carolina State University in 1945. This became an important tie between his research at the Pacific Biological Station and at the University of Hawaii where he went in 1948.

Except for a three-year interval with the U.S. Fish and Wildlife Service, Al was with the Zoology Department of the University of Hawaii from 1948 until his death, from 1958 on as Senior Professor. His many services to the department included a term as Chairman and the planning of its present building, Edmondson Hall. However, Al's departmental colleagues will remember him less for what he did than for what he was — an unfailingly helpful, broad-viewed man who carried more than his share of the day-to-day chores to the time of his death.

His university research began with studies on the life history of tropical baitfish used in the capture of tuna. This led him into the response of tuna to stimuli and factors affecting shark behavior, for which he earned international recognition. In all, he published about 100 papers in a variety of journals. He received the University's Regents Medal for excellence in research in 1974.

Al was happier in research and teaching than in administration. An offer by the Fisheries Research Board in 1948 to assume a senior administrative post may have been a factor in his accepting a professorship in Hawaii. However, in 1955 he became director of the Pacific Oceanic Fisheries Investigations of the U.S. Fish and Wildlife Service in Honolulu and was persuaded in 1957 to serve as chief of the Service's Division of Biological Research in Washington, D.C. After a hectic and somewhat frustrating year in Washington, he decided to return to the more satisfying life of the university in 1958.

From 1967 to 1969 he directed the Cooperative Shark Research and Control Program of the State of Hawaii, and in 1969 he was appointed to the Shark Research Panel of the American Institute of Biological Sciences. He also served as a member of the Governor's Task Force on Hawaii and the Sea and was scientific representative for the Marine Resources Committee of the Pacific Islands Development Commission. Earlier he was President of the Hawaii Chapter of the American Statistical Society.

Al's love of teaching and communicating reached beyond the classroom and the laboratory. He took great delight in interpreting research for public audiences, treating questions from any source with respect and thoughtfulness. In his early years he participated fully in the Nanaimo Kinsmen Club, at which time he was the leader in initiating the annual Nanaimo Fall Fair, and in Honolulu he was active in the Elks Lodge.

Al Tester was a short man with a somewhat dour appearance that was completely belied by a magnificent sense of humor which kept bubbling through at the slightest provocation. He enjoyed meeting old friends and the hospitality in his home at the Crossroads of the Pacific was sincere and abundant. Many will fondly recall the happy times when Al played the organ to a raucous vocal chorus.

Al Tester leaves his wife Laura, his son Murray, his daughter Loretta Fink, and six grandchildren. Al will be widely and greatly missed.

J. CAMERON STEVENSON AND WILLIAM A. GOSLINE

CORRECTIONS TO RECENT PUBLICATIONS
CORRECTIONS SUR RÉCENTS PUBLICATIONS

Volume 21, No. 5 — paper by J. I. Manzer: *Preliminary observations on the vertical distribution of Pacific salmon (genus Oncorhynchus) in the Gulf of Alaska.*

Page 898: line 13, "160 m" should be "60 m."

Page 899: line 1, "160 m" should be "60 m."

Volume 31, No. 5 — paper by P. F. Elson: *Impact of recent economic growth and industrial development on the ecology of Northwest Miramichi Atlantic salmon (Salmo salar).*

Page 528: Figure 5 should be interchanged with Figure 9 (page 533).

Page 544: "Paloheimo, J. E., and P. F. Elson. 1973" reference should be replaced with "Paloheimo, J. E., and P. F. Elson. 1974. Reduction of Atlantic salmon (*Salmo salar*) catches in Canada attributed to the Greenland fishery. J. Fish. Res. Board Can. 31: 1467–1480."

Volume 31, No. 9 — paper by J. E. Paloheimo and P. F. Elson: *Reduction of Atlantic salmon (Salmo salar) catches in Canada attributed to the Greenland fishery.*

Page 1469: Figure 2, caption should read "Total landings (commercial and angling) in New Brunswick and Nova Scotia from 1952 to 1971"; Figure 2, label for Y-axis should read "Total New Brunswick catches in '00000 pounds."

Page 1473: Right column, lines 2 and 3, "16–24%" and "20–52%" should read "13–24%" and "15–52%."

Page 1476: Table 14, Part B, "$r^2 = 0.694$" should read "$r^2 = 0.0694$."

Page 1477: Right column, delete line 6 beginning "The 20% figure which agrees ..." and ending on p. 1478, Left column, line 2, "... essentially unaltered."

Page 1478: Figure 4, Y-axis should read "in '00000 pounds" instead of "in hundreds."

Page 1439: Table 19, second section, "B:" should be inserted.

Volume 32, No. 2 — note by D. D. Sameoto, D. C. Darrow, and S. Guildford: *DDT residues in euphausiids in the upper estuary of the Gulf of St. Lawrence.*

Page 313: The following reference should be included: "Holden, A. V., and K. Marsden. 1967. Organochlorine pesticides in seals and porpoises. Nature 216: 1274–1276."

Volume 32, No. 2 — note by M. Paradis and R. G. Ackman: *Differentiation between natural hydrocarbons and low level diesel oil contamination in cooked lobster meat.*

Page 316, Résumé: Il a fallu combiner l'extraction des lipides totaux, la chromatographie sur colonne et la chromatographie à température programmée pour démontrer une faible contamination contestée d'essence-Diesel dans de la chair de homard cuite. On a pu démontrer la présence d'essence-Diesel comme contaminant spécifique, mais les composants identifiables ne dépassaient pas de beaucoup les mêmes composants considérés comme arrière-goût normal dans de la chair de homard en conserve organoleptiquement acceptable.

Volume 32, No. 4 — paper by D. S. Cherry, K. L. Dickson, and J. Cairns Jr.: *Temperatures selected and avoided by fish at various acclimation temperatures.*

Addendum: Cyprinids tested ranged from 1 to 3 age-classes and preliminary testing of responses between sexes was conducted with fish from these age-groups. Some trials conducted with *Nocomis leptocephalus* may have contained mixed groups of *N. leptocephalus* and *N. playrhynchus.*

Volume 32, No. 5 — note by S. A. Poulet and J. P. Chanut: *Nonselective feeding of Pseudocalanus minutus.*

Page 707: Table 1, headnote, line 3, "$\text{mg} \times \text{L}^{-1} \times \text{copepod}^{-1} \times \text{h}^{-1}$" should read "$\text{mg} \times 10^{-4} \times \text{copepod}^{-1} \times \text{h}^{-1}$."

Volume 32, No. 6 — perspective by E. K. Balon: *Reproductive guilds of fishes: a proposal and definition.*

Page 832: Left column, line 33, "*C. sardinella*" should read "*C. albula sardinella*"; line 50, delete "*Abramis ballerus.*"

Page 834: Left column, line 23 should read "Europe: *Abramis ballerus*, *A. brama*, *Alburnus alburnus*"; line 26, "*L. soufia*" should read "*L. souffia*"; lines 27 and 28 should read "*Rutilus rutilus* and its migratory morphs *R. frisi frisi*", Right column, line 27, "*Blicca bjoerkna*" should read "*Abramis bjoerkna*"; line 28, delete "*gibelio.*"

Page 835: Left column, line 21, "*Nemacheilus barbatulus*" should read "*Noemacheilus barbatulus.*"

Page 838: Right column, lines 1–5 should read "Cyprinid fish genera, like *Acanthorhodeus, Rhodeus, Acheilognathus, Paracheilognathus, Pseudoperilampus,* and *Tanakia* deposit their eggs in ..."

Page 842: Right column, line 36, "*Ophiocephalus* spp." should read "*Channa* spp."

Page 858: Table 2, Guild A, 1.3 and 1.4 data for Danube River should be 10 and 12 instead of 11 and 11, and for Europe, 40 and 24 instead of 41 and 23.

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

The role of stock biomass and temperature in the recruitment of southern Gulf of St. Lawrence Atlantic cod, *Gadus morhua* **P. F. Lett, A. C. Kohler, and D. N. Fitzgerald**

A simple method for predicting the capacity of a lake for development based on lake trophic status **P. J. Dillon and F. H. Rigler**

Solubilization of cod myofibrillar proteins at low ionic strength by sodium pyruvate during frozen storage **V. D. Tran**

Blood oxygen dissociation characterisitic of the winter flounder, *Pseudopleuronectes americanus* **J. B. Hayden, J. J. Cech Jr., and D. W. Bridges**

A periscopic method for determining the three dimensional positions of fish in schools **T. J. Pitcher**

Annual and longer term variations of deepwater properties in the coastal waters of southern British Columbia **G. L. Pickard**

Respiration and chemical composition of *Pleuroncodes planipes* (Decapoda: Galatheidae): energetic significance in an upwelling system **K. L. Smith Jr., G. R. Harbison, G. T. Rowe, and C. H. Clifford**

Temperature and deteriorative changes in postrigor cod muscle stored up to 14 days in the superchill range, −1 to −4 C **S. S. S. Nowlan, W. J. Dyer, and R. A. Keith**

Experimental observations of predation by goldfish (*Carassius carassius*) on the zooplankton of a small saline lake **C. P. Archibald**

Relation of water temperature to Ceratomyxosis in rainbow trout (*Salmo gairdneri*) and coho salmon (*Oncorhynchus kisutch*) **L. R. Udey, J. L. Fryer, and K. S. Pilcher**

Relation of water temperature to *Flexibacter columnaris* infection in steelhead trout (*Salmo gairdneri*), coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon **R. A. Holt, J. E. Sanders, J. L. Zinn, J. L. Fryer, and K. S. Pilcher**

Notes

Biosynthesis of lecithin by the CDP–choline pathway in liver microsomes of rainbow trout, *Salmo gairdneri* **B. J. Holub, K. Nilsson, J. Piekarski, and S. J. Slinger**

Utilization of wastes from lumpfish, *Cyclopterus lumpus*, roe harvesting operations: an examination of the lipid and glue potential, and comparison of meal with that from Nova Scotia-caught menhaden **M. Paradis, R. G. Ackman, J. Hingley, and C. A. Eaton**

Ceratomyxa shasta (Myxosporida) disease in chum salmon (*Oncorhynchus keta*) in British Columbia **L. Margolis and T. P. T. Evelyn**

Mortality of *Transennella tantilla* due to burial **V. F. Galluchi and R. K. Kawaratani**

Phoma herbarum, a fungal plant saprophyte, as a fish pathogen **A. J. Ross, W. T. Yasutake, and S. Leek**

Selection by brook trout (*Salvelinus fontinalis*) and juvenile Atlantic salmon (*Salmo salar*) of shade related to water depth **R. J. Gibson and G. Power**

Perspectives

Benthic organisms and the structure of marine ecosystems **E. R. Mills**

The terminology of intervals in fish development **E. K. Balon**

Book Reviews/Comptes rendus

Modelling the eutrophication process (E. J. Middlebrooks, D. H. Falkenborg, and T. E. Maloney [ed.]) **D. W. Schindler**

Freedom of oceanic research (W. S. Wooster [ed.]) **J. C. Marr**

Genetics and mutagenesis of fish (J. H. Schröder [ed.]) **W. K. Hershberger**

Chemoreception in marine organisms (P. T. Grant and A. M. Mackie [ed.]) **D. W. McLeese**

Fish immunology (D. P. Anderson) **G. B. Pauley**

RECENT PUBLICATIONS / RÉCENTES PUBLICATIONS

The number following each title in each series refers to the establishments listed at the end of the section.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section.

Recent Studies

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles on investigations published in other periodicals, which henceforth may be obtained in reprint form only from the author or originating establishment.

Récentes études

Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n° 1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes d'études sur des recherches mentionnées dans d'autres périodiques. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

2046. Willis, D. E., and R. F. Addison. 1974. Hydroxylation of biphenyl *in vitro* by tissue preparations of some marine organisms. Comp. Gen. Pharmacol. 5: 77–81. (7)

2047. Addison, R. F. 1974. Estimation of *N*-ethyl *O*-isopropyl thionocarbamate (Dow: Z-200) in mine wastes by GLC. Int. J. Environ. Anal. Chem. 3: 287–292. (7)

2048. Addison, R. F., and T. G. Smith. 1974. Organochlorine residue levels in Arctic ringed seals: variation with age and sex. Oikos: 25: 335–337. (7)

2049. Zitko, V., W. V. Carson, and W. G. Carson. 1975. Thallium: occurrence in the environment and toxicity to fish. Bull. Environ. Contam. Toxicol. 13: 23–30. (6)

2050. Hara, T. J., and S. MacDonald. 1975. Morpholine as olfactory stimulus in fish. Science 187: 81–82. (4)

2051. Schindler, D. W., and E. J. Fee. 1974. Primary production in freshwater. Proc. First Int. Congr. Ecology. Sept. 8–14, 1974. p. 155–158. (4)

2052. Bilton, H. T. 1973. Effects of starvation and feeding on circulus formation on scales of young sockeye salmon of four racial origins, and of one race of young kokanee, coho and chinook salmon. Proc. Symp. Ageing of Fish, July 19–20, 1973. p. 40–70. (1)

2053. Sergeant, D. E. 1974. Seasonal distribution of bowhead and white whales in the eastern Beaufort Sea. Proc. Symp. Beaufort Sea Coast and Shelf Research, Jan. 9, 1974. p. 705–719. (5)

2054. Grainger, E. H. 1974. Nutrients in the southern Beaufort Sea. Proc. Symp. Beaufort Sea Coast and Shelf Research. Jan. 9, 1974. p. 589–606. (5)

2055. Wacasey, J. W. 1974. Zoobenthos of the southern Beaufort Sea. Proc. Symp. Beaufort Sea Coast and Shelf Research. Jan. 9, 1974. p. 697–704. (5)

2056. Bilinski, E., and R. E. E. Jonas. 1975. Correlation between the freshness of iced salmonids and lactic acid formation in muscle extracts. J. Food Sci. 40: 53–57. (2)

2057. Sangalang, G. B., and H. C. Freeman. 1974. Effects of sublethal cadmium on maturation and testosterone and 11-ketotestosterone production *in vivo* in brook trout. Biol. Reprod. 11: 429–435. (8)

2058. Ackman, R. G. 1974. Myocardial alterations resulting from feeding partially hydrogenated marine oils and peanut oil to rats. Lipids 9: 1032–1035. (8)

2059. Sekerak, A. K., and H. P. Arai. 1974. A revision of *Helicometra* Odhner, 1902 and related genera (Trematoda: Opecoelidae), including a description of *Neohelicometra sebastis* n. sp. Can. J. Zool. 52: 707–738. (1)

2060. Forrester, C. R., and D. F. Alderdice. 1973. Laboratory observations on early development of the Pacific halibut. Int. Pac. Halibut Comm. Tech. Rep. 9: 13 p. (1)

2061. Ricker, W. E., and H. H. Ross. 1975. Synopsis of the Brachypterinae, (Insecta: Plecoptera: Taeniopterygidae). Can. J. Zool. 53: 132–153. (1)

2062. Lindsey, J. K. 1974. Comparison of probability distributions. J. R. Stat. Soc. 1: 38–47. (1)

2063. Levings, C. D. 1974. Seasonal changes in feeding and particle selection by winter flounder (*Pseudopleuronectes americanus*). Trans. Am. Fish. Soc. 103: 828–832. (3)

2064. MacNeill, I. B., and R. G. Dowd. 1975. Analysis of fish count data obtained using a digital echo counting system. Appl. Stat. 1975: 247–260. (7)

2065. Gordon, D. C. Jr., P. D. Keizer, and J. Dale. 1974. Estimates using fluorescence spectroscopy of the present state of petroleum hydrocarbon contamination in the water column of the northwest Atlantic Ocean. Mar. Chem. 2: 251–261. (7)

2066. Brett, J. R. 1974. Tank experiments on the culture of pan-size sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) using environmental control. Aquaculture 4: 341–352. (1)

2067. Cheng, J. Y., M. Don-Paul, and N. J. Antia. 1974. Isolation of an unusually stable *Cis*-isomer of alloxanthin from a bleached autolysed culture of *Chroomonas salina* grown photoheterotrophically on glycerol. Observations on *Cis-Trans* isomerization of alloxanthin. J. Protozool. 21: 761–768. (2)

2068. Antia, N. J., R. F. Lee, J. C. Nevenzel, and J. Y.

CHENG. 1974. Wax ester production by the marine cryptomonad *Chroomonas salina* grown photoheterotrophically on glycerol. J. Protozool. 21: 768–771. (2)

2069. BROCKERHOFF, H. 1974. Lipolytic enzymes. Adv. Chem. Ser. 136: 131–145. (8)

2070. ACKMAN, R. G., AND C. A. EATON. 1975. Lipids of freshwater dolphin *Sotalia fluviatilis*: comparison of odontocete bioacoustic lipids and habitat. Lipids 10: 44–49. (8)

2071. ACKMAN, R. G., AND M. HARRINGTON. 1975. Fishery products as components of diets restricted in phytanic acid for patients with Refsum's syndrome. J. Can. Diet. Assoc. 31(1): 4 p. (8)

2072. PARADIS, M., AND R. G. ACKMAN. 1975. Occurrence and chemical structure of nonmethylene-interrupted dienoic fatty acids in American oyster *Crassostrea virginica*. Lipids 10: 12–16. (8)

2073. LI, M. F., AND G. S. TRAXLER. 1974. Effect of mercuric chloride on cellular morphology and acid phosphatase of tissue culture cells cultivated in suspension. Environ. Physiol. Biochem. 4: 263–269. (8)

2074. SNOW, N. B., AND B. F. SCOTT. 1975. The effect and fate of crude oil spilt on two Arctic lakes. Proc. Conf. Prevention and Control of Oil Pollution, March 25–27, 1975. p. 527–534. (4)

2075. CONOVER, R. J. 1974. Production in marine planktonic communities, p. 159–163. *In* A. J. Cavé (Congress secretary) Proc. First Int. Congr. Ecol., Sept. 8–14, The Hague, Neth. (7)

2076. LOCKHART, W. L., D. A. METNER, AND N. GRIFT. 1973. Biochemical and residue studies on rainbow trout (*Salmo gairdneri*) following field and laboratory exposures to fenitrothion. Manit. Entomol. 7: 26–36. (4)

2077. FLANNAGAN, J. F. 1973. Field and laboratory studies of the effect of exposure to fenitrothion on freshwater aquatic invertebrates. Manit. Entomol. 7: 15–25. (4)

2078. SCHINDLER, D. W. 1973. Nutrients in a lake, p. 175–182. *In* N. Calder [ed.] A guide to environmental science. Wedendeld and Nicolson, London. (4)

2079. BEAMISH, P. 1974. Whale acoustics. Acoustics and noise control in Canada. J. Can. Acoust. Assoc. 2: 8–12. (7)

Interpretive Articles Series

This new series commenced in 1966. The articles interpret work already published in primary journals. They appear at irregular intervals in various technical publications. Frequently an article essentially duplicates, condenses, or is based on an article in another series.

Articles explicatifs

Cette série a débuté en 1966. Les articles donnent une explication de travaux déjà publiés dans des revues de fonds. Ils paraissent à intervalles irréguliers, dans diverses publications techniques. Souvent, un article se basera sur un écrit d'une autre série, le condensera ou le reproduira presque tel quel.

324. WALDICHUK, M. 1974. Some biological concerns in heavy metals pollution, p. 1–57. *In* Pollution and physiology of marine organisms. Academic Press, Inc., New York, N.Y. (3)

325. SANDEMAN, E. J. 1974. Offshore renewable resources and their management. Can. Ship. Mar. Engineer. 45(7): 29–31. (9)

326. DOWD, R. G. 1974. A computerized echo counting system for demersal fishes. Compiled by Edmunde Newhall Assoc. Ltd., and Montreal Eng. Co. Ltd. 196p. (7)

327. KABATA, Z. 1974. Book review of: Parasites and diseases of fishes and aquatic invertebrates by O. N. Bauer [ed.] 1972. Nauka, Moscow, USSR. 173 p. J. Fish. Biol. 6: p. 541. (1)

Manuscript Reports

This series includes unpublished preliminary reports and data records not intended for general distribution. They should not be referred to in publications without clearance from the issuing establishment and without clear indication of their manuscript status.

Rapports manuscrits

La série comprend des articles d'information et des rapports préliminaires non publiés, qui ne sont pas destinés à la distribution générale. Ils ne doivent pas être donnés en références sans l'assentiment du service dépositaire et sans une indication claire de leur forme manuscrite.

BRAY, J. R. 1975. Marine fish surveys in the Mackenzie delta area. Fish. Res. Board Can. MS Rep. 1326: 10 p. (5)

ZITKO, V., AND W. G. CARSON. 1974. Avoidance of organic solvents and substituted phenols by juvenile Atlantic salmon. Fish. Res. Board Can. MS Rep. 1327: 15 p. (6)

ARO, K. V. 1974. Recoveries of salmon tagged offshore in the North Pacific Ocean by Japan and the United States in 1972 and 1973, and additional recoveries from earlier taggings by Canada, Japan, and the United States. Fish. Res. Board Can. MS Rep. 1328: 20 p. (1)

KRISTMANSON, D. D. 1974. Salinity distributions in the Musquash estuary. Fish. Res. Board Can. MS Rep. 1329: 49 p. (6)

WESTRHEIM, S. J. 1974. U.S.S.R. interpretations of Pacific ocean perch otoliths and scales collected in Queen Charlotte Sound during June 1972. Fish. Res. Board Can. MS Rep. 1330: 7 p. (1)

PARKER, R. R. AND B. A. KASK. 1974. Fishes of the Nanaimo Estuary, their species composition, abundance, and diet, July 1972 – March 1973. (data record). Fish. Res. Board Can. MS Rep. 1331: 307 p. (1)

McInnes, B. E., F. W. Nash, and H. Godfrey. 1974. A preliminary annotated bibliography on Georgia Strait fishes. Fish. Res. Board Can. MS Rep. 1332: 216 p. (1)

Day, D. 1974. Proceedings of the Pacific coast herring workshop. Fish. Res. Board Can. MS Rep. 1333: 35 p. (1)

Hackie, D. A. 1974. Station reprints 1969–1973. Suppl. 3. Fish. Res. Board Can. MS Rep. 1334: 18 p. (2)

Hunter, J. G. 1975. Fishery resources of the western arctic. Fish. Res. Board Can. MS Rep. 1335: 33 p. (5)

Smith, M. S. 1975. *A. P. Knight* groundfish cruise no. 74-2, October 15–17, 1974 (Data record). Fish. Res. Board Can. MS Rep. 1336: 13 p. (1)

Bigg, M. A., and I. B. MacAskie. 1975. Report on Canadian pelagic fur seal research in 1973–1974. Fish. Res. Board Can. MS Rep. 1337: 20 p. (1)

Kennedy, O. D., and R. J. LeBrasseur. 1975. Zooplankton, species counts in vertical hauls in Great Central lake, 1973. Fish. Res. Board Can. MS Rep. 1338: 59 p. (1)

Kennedy, O. D., and R. J. LeBrasseur. 1975. Zooplankton, species counts for Stamp River and Ash River drainage diversion, 1973. Fish. Res. Board Can. MS Rep. 1339: 154 p. (1)

Nash, F. W., and J. A. Thomson. 1975. A catalogue of programs in the computing center, Pacific Biological Station. Fish. Res. Board Can. MS rep. 1340: (1)

Chilton, D. E., and J. E. Smith. 1975. Data record: Pacific cod (*Gadus macrocephalus*). A. Catch statistics of the Canadian and United States trawl fishery, 1966–73. B. Length composition of commercial landings by Canadian trawlers, 1967–73. Fish. Res. Board Can. MS. Rep. 1341: (1)

Outram, D. N. 1975. Proceedings of the second annual Pacific coast herring workshop, October 30–31, 1974. Fish. Res. Board Can. MS Rep. 1342: (1)

Chilton, D. E. 1975. An inventory of biological samples taken in the commercial groundfish fishery in British Columbia in 1974 (data record). Fish. Res. Board Can. MS Rep. 1343: (1)

Westrheim. S. W., and C. R. Forrester. 1975. Pacific cod tagging. I. Inventory of experiments and analysis of tag-type comparisons. Fish. Res. Board Can. MS Rep. 1344: (1)

Levings, C. D., W. M. Pomeroy, and R. Prange. 1975. Sampling locations for intertidal biota and preliminary observations of habitats at some British Columbia estuaries. Fish. Res. Board Can. MS Rep. 1345: (1)

Technical Report Series

Technical Reports are research documents that are of sufficient importance to be preserved, but which for some reason are not appropriate for primary scientific publication. Inquiries concerning any particular Report should be directed to the issuing establishment.

Rapports techniques

Les rapports techniques sont des documents de recherche qui revêtent une assez grande importance pour être conservés mais qui, pour une raison ou pour une autre, ne conviennent pas à une publication scientifique de fonds. Pour toute demande de renseignements concernant un rapport particulier, il faut s'adresser au service responsable.

492. Brinckmann-Voss, A. 1974. British Columbia marine faunistic survey report on the Hydrozoa: Part I. Medusae. Fish. Mar. Serv. Res. Dev. Tech. Rep. 492: 21 p. (1)
493. Alderdice, D. F., and J. A. Thomson. 1974. Characteristics of some modified second-order orthogonal composite factorial designs. Fish. Mar. Serv. Res. Dev. Tech. Rep. 493: 70 p. (1)
494. Parker, R. R., B. A. Kask, and B. Windecker. 1975. Vertical distribution of macrozooplankton in respect to the halocline, Alberni Inlet, during April, June, and August 1971. An atlas. Fish. Mar. Serv. Res. Dev. Tech. Rep. 494: (1)
495. Nowak, S. H. 1974. A solid state temperature controller with heating and cooling control. Fish. Mar. Serv. Res. Dev. Tech. Rep. 495: 16 p. (4)
496. Barner, L. W., and F. H. C. Taylor. 1975. The offshore herring survey off southwest Vancouver Island in 1972 and 1973. Report on *G. B. Reed* cruises GBR 72-4 (October 18 – November 2), GBR 73-1 (January 17–31), and GBR 73-2 (March 13–29). Fish. Mar. Serv. Res. Dev. Tech. Rep. 496: (1)
497. Westrheim, S. J., W. R. Harling, D. Davenport, and M. S. Smith. 1974. *G. B. Reed* groundfish cruise no. 74-4, September 4–25, 1974 (Data record). Fish. Mar. Serv. Res. Dev. Tech. Rep. 497: 37 p. (1)
498. Pannekoek, W. J., J. P. Kelsall, and R. Burton. 1975. Methods of analyzing feathers for elemental content. Fish. Mar. Serv. Res. Dev. Tech. Rep. 498: (1)
499. Pincock, D. G., D. McG. Luke, D. W. Church, and A. B. Stasko. 1974. An automatic monitor for detecting and recording passage of transmitter-fitted fish. Fish. Mar. Serv. Res. Dev. Tech. Rep. 499: 59 p. (6)
500. Freeman, K. 1974. Growth, mortality, and seasonal cycle of *Mytilus edulis* in two Nova Scotian embayments. Fish. Mar. Serv. Res. Dev. Tech. Rep. 500: 112 p. (7)
501. Griffioen, W., and D. W. Narver. 1974. A note on winter starvation and feeding of cultured juvenile coho salmon. Fish. Mar. Serv. Res. Dev. Tech. Rep. 501: 24 p. (1)
502. Lawrence, M., and E. Scherer. 1974. Behavioural responses of whitefish and rainbow trout to drilling fluids. Fish. Mar. Serv. Res. Dev. Tech. Rep. 502: 47 p. (4)

503. Taylor, F. H. C., and L. W. Barner. 1975. A herring survey of Juan de Fuca Strait in 1971. Report on *A. P. Knight* cruises APK 73-3, -4, -5, -6, and -7 (July 22 – December 12). Fish. Mar. Serv. Res. Dev. Tech. Rep. 503: (1)
504. Nicholson, H. F. 1975. Bibliography on the limnology and fisheries of Canadian freshwaters — No. 2. Fish. Mar. Serv. Res. Dev. Tech. Rep. 504: 113 p. (11)
505. Marshall, K. E. 1975. An index to the publications of the staff of the Freshwater Institute, Winnipeg; the biological station and technical unit, London; and the central biological station, Winnipeg: 1944–1973. Fish. Mar. Serv. Res. Dev. Tech. Rep. 505: 94 p. (4)
506. Thompson, J. A. J., and D. W. Paton. 1975. Chemical delineation of a submerged mine tailings plume in Rupert and Holberg Inlets, B.C. Fish. Mar. Serv. Res. Dev. Tech. Rep. 506: (3)
507. Mansfield, A. W., D. E. Sergeant, and T. G. Smith. 1975. Marine mammal research in the Canadian arctic. Fish. Mar. Serv. Res. Dev. Tech. Rep. 507: 23 p. (5)
508. Velsen, F. P. J. 1974. Constant-flow dosing apparatus. Fish. Mar. Serv. Res. Dev. Tech. Rep. 508: 13 p. (1)
509. Whyte, J. N. C., and J. R. Englar. 1974. Elemental composition of the marine alga *Nereocystis leutkeana* over the growing season. Fish. Mar. Serv. Res. Dev. Tech. Rep. 509: 29 p. (2)
510. Sunde, L. A., and J. Barica. 1975. Geography and lake morphometry of the aquaculture study area in the Erickson–Elphinstone district of southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 510: 35 p. (4)
511. Barica, J. 1975. Geochemistry and nutrient regime of saline eutrophic lakes in the Erickson–Elphinstone district of southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 511: 82 p. (4)
512. Kling, H. 1975. Phytoplankton successions and species distribution in prairie ponds of the Erickson–Elphinstone district, southwestern Manitoba. Fish. Mar. Serv. Res. Dev. Tech. Rep. 512: 31 p. (4)
513. Findlay, D. L., and H. J. Kling. 1975. Seasonal successions of phytoplankton in seven lake basins in the Experimental Lakes Area, northwestern Ontario, following artificial eutrophication. Fish. Mar. Serv. Res. Dev. Tech. Rep. 513: 53 p. (4)
514. Bilinski, E., R. E. E. Jonas, and Y. C. Lau. 1975. Canned herring fillets with sauces. Survey and characterization of commercial products. Fish. Mar. Serv. Res. Dev. Tech. Rep. 514: 20 p. (2)
515. Scarsbrook, F. R., and J. McDonald. 1975. Purse seine catches of sockeye salmon (*Oncorhynchus nerka*) and other species of fish at Babine Lake, British Columbia, 1973 (Data record). Fish. Mar. Serv. Res. Dev. Tech. Rep. 515: (1)
516. Stockner, J. G., and D. D. Cliff. 1975. Marine phytoplankton production, distribution and species composition in Pendrell and Hotham sounds, British Columbia. Fish. Mar. Serv. Res. Dev. Tech. Rep. 516: (2)
517. Townsend, B. E., B. Van der Veen, and J. F. Flannagan. 1975. Electronic systems for the continual monitoring of temperature, pH, conductivity and dissolved oxygen. Fish. Mar. Serv. Res. Dev. Tech. Rep. 517: 15 p. (4)
518. Zitko, V. 1975. Chemistry, applications, toxicity, and pollution potential of thallium. Fish. Mar. Serv. Res. Dev. Tech. Rep. 518: 41 p. (6)
519. Otte, G. 1975. A laboratory key for the identification of *Corophium* species (Amphopoda, Corophiidae) of British Columbia. Fish. Mar. Serv. Res. Dev. Tech. Rep. 519: (3)
520. Doubleday, W. G. 1975. Two computer programs for analysis of catch at age data. Fish. Mar. Serv. Res. Dev. Tech. Rep. 520: (6)
521. Kohler, A. C., D. J. Faber, and N. J. McFarlane. 1975. Eggs, larvae and juveniles of fishes from plankton collections in the Gulf of St. Lawrence during 1969. Fish. Mar. Serv. Res. Dev. Tech. Rep. 521: (6)
522. Wickett, W. P., and J. A. Thomson. 1975. Transport computations for the North Pacific Ocean, 1973. Fish. Mar. Serv. Res. Dev. Tech. Rep. 522: (1)
523. Platt, T., K. L. Denman, and A. D. Jassby. 1975. The mathematical representation and prediction of phytoplankton productivity. Fish. Mar. Serv. Res. Dev. Tech. Rep. 523: 110 p. (7)
524. Subba Rao, D. V. 1975. Phytoplankton production, nutrients and density structure in the shelf area of Nova Scotia and Georges Bank during August, 1974. Fish. Mar. Serv. Res. Dev. Tech. Rep. 524: 265 p. (7)
525. Watson, N. H. F., H. F. Nicholson, and L. R. Culp. 1975. Chlorophyll *A* and primary production in Lake Superior, May to November, 1973. Fish. Mar. Serv. Res. Dev. Tech. Rep. 525: (11)
526. Pinhorn, A. T., and R. J. Halliday. 1975. Resources 1975 — current status of Atlantic offshore groundfish stocks and fisheries. Fish. Mar. Serv. Res. Dev. Tech. Rep. 526: (9)
527. Machniak, K. 1975. The effects of hydroelectric development on the biology of northern fishes (reproduction and population dynamics) I. Lake whitefish *Coregonus clupeaformis* (Mitchell). A literature review and bibliography. Fish. Mar. Serv. Res. Dev. Tech. Rep. 527: (4)
528. Machniak, K. 1975. The effects of hydroelectric development on the biology of northern fishes (Reproduction and population dynamics) II. Northern pike *Esox lucius* (Linnaeus). A literature review and bibliography. Fish. Mar. Serv. Res. Dev. Tech. Rep. 528: (4)
529. Machniak, K. 1975. The effects of hydroelectric development on the biology of northern fishes (Reproduction and population dynamics) III. Yellow walleye *Stizostedion vitreum vitreum* (Mitchell). A literature review and bibliography. Fish. Mar. Serv. Res. Dev. Tech. Rep. 529: (4)
530. Machniak, K. 1975. The effects of hydroelectric development on the biology of northern fishes. (Reproduction and population dynamics) IV.

Lake trout *Salvelinus namaycush* (Walbaum). A literature review and bibliography. Fish. Mar. Serv. Res. Dev. Tech. Rep. 530: (4)

531. Sutterlin, A. M., and S. Waddy. 1975. Harvesting, processing, and composition of sea cucumber meal as a possible substitution for herring meal in trout diets. Fish. Mar. Serv. Res. Dev. Tech. Rep. 532: (6)

532. Scarratt, D. J. 1975. Observations of lobsters and scallops near Pictou, N.S. Fish. Mar. Serv. Res. Dev. Tech. Rep. 532: (6)

533. Healey, M. C., and H. J. Kling. 1975 Experimental cropping of lakes. 3. Phytoplankton and zooplankton. Fish. Mar. Serv. Res. Dev. Tech. Rep. 533: (1)

534. Stasko, A. B. 1975. Annotated bibliography of underwater biotelemetry. Fish Mar. Serv. Res. Dev. Tech. Rep. 534: (6)

535. Peters, M. D., and R. J. Bose. 1975. clinoptilolite—a physico-chemical approach to ammonia removal in hatchery and aquaculture water reuse systems. Fish. Mar. Serv. Res. Dev. Tech. Rep. 535: (2)

Translation Series

The following translations have been prepared by or for the Fisheries and Marine Service, for use in its investigations. Copies are available from Translation Services, Canada Institute for Scientific and Technical Information, National Research Council of Canada, Ottawa, Ontario K1A 0S2, at a cost of 10c per page and a minimum charge of $1.00. Information on translations can generally be obtained from the Office of the Editor.

Traductions

Les traductions dont il est question ci-après ont été préparées par ou pour le Service des pêches et des sciences de la mer, à des fins de recherche. On peut en obtenir des exemplaires, à 10 cents la page et à un prix minimum de un dollar, aux Services de traduction, Institut canadien de l'information scientifique et technologique, Conseil national de recherches du Canada, Ottawa (Ontario), K1A 0S2. Le Bureau du rédacteur peut en général fournir des renseignements sur ces traductions.

Nagayama, F., Y. Saito, and M. Hayashi. 1967. Distribution of β-glucuronidase in fish. Nippon Suisan Gakkaishi 33: 1132–1135. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3339, 1975)

Ishino, T. 1974. Procedures for the removal of mercury from fish meat. Kagaku Kogyo 25: 411–421. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3340, 1975)

Anon. 1944. Concerning the reproduction of the ocean perch. Tr. Polyarn. Nauchno-Issled. Proektn. Inst. Morsk. Rybn. Khoz. Okeanogr. 8: 280–306. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3341, 1975)

Kobashi, K., S. Takebe, and J. Hase. 1973. Distribution, metabolism and excretion of caprylo- and nicotino-hydroxamic acid. Yakugaku Zasshi 93: 1564–1572. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3342, 1975)

San-Wen, W., Y. Gan-yung, Y. Pei-chi, and H. Hung-jean. 1964. Record of economic animals of China freshwater fishes. China Publishing Co. 8 p. (Transl. from Chinese by Fish. Mar. Serv. Transl. Ser. No. 3343, 1975)

Wieser, W., and G. Schweizer. 1972. Contents of ammonia and of free amino acids, and the properties of a glutaminase in *Porcellio scaber* (Isopoda). J. Comp. Physiol. 81: 73–88. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3344, 1975)

Fedorov, V. V. 1973. Ichthyofauna of the continental slope of the Bering Sea and some aspects of its origin and formation. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 87: 3–41. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3345, 1975)

Grishina, N. L., and D. I. Kuznetsov. 1974. Rapid extraction-gravimetric method for the quantitative determination of lipids in fish and fish products. Rybn. Khoz. (Moscow) 4: 67–68. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3346, 1975)

Minder, L. P. 1948. The brining method and the rate of fish salting. Rybn. Khoz. 24: 42–43. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3347, 1975)

Doering, C. E., D. Estel, R. Geyer, and W. H. Wendt. 1974. Capillary gas chromatographic investigation of straight-chain C dienes. Z. Chem. 14: 292–293. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3348, 1975)

Grob, K. 1974. Current limitations of high resolution gas chromatography. Chromatographia 7: 94–98. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3349, 1975)

Tsukuda, N., and T. Kitahara. 1974. Composition of the esterified fatty acids of astaxanthin diester in the skin of seven red fishes. Tokaiku Suisan Kenkyusho Kenkyu Hokoku 77: 89–95. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3350, 1975)

Stosch, H.-A. [Undated]. The centric bottom diatoms. Helgol. Wiss. Meeresunters. 5: 273–291. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3351, 1975)

Ernst, W., and H. Goerke. 1974. Adenosine-5′-triphosphate (ATP) in sediments and nematodes of the northeastern Atlantic deep-sea. "Meteor" Forschungersergeb. Reihe C 18: 35–42. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3352, 1975)

Ooyama, S. 1973. Studies on the odor of canned fish (Part 1) Volatile components from the muscle of fresh fish. Kaseigaku Zasshi 24: 694–698. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3353, 1975)

ITOH, K. 1973. Food requirements of copepods estimated from their metabolic rates. Nippu kai ho 20: 78–83. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3354, 1975)

KUBACKI, S. J., W. KASPROWICZ, M. JANIOLKOWSKA, AND T. PISKORZ. 1973. Determination of higher fatty acids in edible vegetable fats. Pr. Inst. Lab. Badaw. Przem. Spozyw. 23: 535–555. (Transl. from Polish by Fish. Mar. Serv. Transl. Ser. No. 3355, 1975)

LISOVSKAYA, V. I., AND A. G. RUDENKO. 1973. Study of the lipid content of the liver of some epipelagic commercial fishes. Biol. Morya (30): 119–124. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3356, 1975)

LEVANIDOV, I. 1940. Accelerated methods of processing herring. Rybn. Khoz. 16: 8–11. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3357, 1975)

ZHUKOV, A. V., AND A. G. VERESHCHAGIN. 1974. Set-up for the quantitative extraction of lipids from plant material. Fiziol. Rast. 21: 659–663. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3358, 1975)

MIRONOVA, V. N., R. P. KANDYUK, AND V. M. KLIMASHEVSKII. 1973. The content of sterols in the liver of south Atlantic fishes. Biol. Morya 30: 137–140. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3359, 1975)

VINOGRADOVA, Z. A., AND R. P. MOROZOVA. 1973. Study of the oxidation products of 7-dehydrocholesterol in unsaponified liver fraction of some fishes of the equatorial Atlantic. Biol. Morya 30: 140–145. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3360, 1975)

LEVANIDOV, I. P. 1948. The diffusion of salt and the rate of fish salting. Rybn. Khoz. 24: 33–39. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3361, 1975)

NOVIKOV, YU. V. 1973. Some peculiarities of the study of the breeding ecology of the saury and other fishes of the Kuroshio waters community. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 87: 155–162. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3362, 1975)

GRADL, T. 1974. Enzymatic in situ measurements (New measuring methods for sea water and sediment). Kiel. Meeresforsch. 30: 1–11. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3363, 1975)

OBA, T., H. ITO, AND S. MIZUMACHI. 1973. GLC determination of phthalate esters eluted from PVC medical devices made from vinyl chloride resin. Eisei Shikenjo Hokoku 91: 1–4. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3364, 1975)

FEDOSEEV, G. A. 1973. Morphological–ecological characteristics of ribbon seal populations and factors affecting the conservation of usable stocks. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 86: 158–177. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3365, 1975)

LÓPEZ-BENITO, M., AND G. SAMPEDRO. 1973. Skinning of frozen hake, horse mackerel, mackerel and sardines with alkaline bath of sodium hydroxide. Informes técnicos del Instituto de Investigaciones Pesqueras 6: 1–12. (Transl. from Spanish by Fish. Mar. Serv. Transl. Ser. No. 3366, 1975)

BREZEANU, G. 1972. Food and trophic relations in Stizostedion-Lucioperca larvae and juveniles in natural and experimental conditions. Bul. Cercet. Piscic. 31: 35–46. (Transl. from Romanian by Fish. Mar. Serv. Transl. Ser. No. 3367, 1975)

PETIPA, T. S., A. V. MONAKOV, A. P. PAVLYUTIN, AND YU. I. SOROKIN. 1974. The significance of detritus and humus in the nutrition and energy balance of the copepod *Undinula darwini* Scott. Biologicheskaya produktivnost' yuzhnykh morei 1974: 153–160. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3368, 1975)

FEDOSEEV, G. A. 1965. The ecology of the reproduction of seals in the northern part of the Sea of Okhotsk. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 65: 212–216. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3369, 1975)

URICH, K., U. HERZ-HUBNER, and U. SPECK. 1973. The metabolic fate of nutrients in the crayfish, *Orconectes limosus*. V. Chemical conversion of glucose within the absorbing tissues. J. Comp. Physiol. 86: 187–191. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3370, 1975)

OTA, T., AND M. YAMADA. 1974. Lipids of Masu salmon. II. Seasonal variations of the lipids in the flesh of Masu salmon parr during the fresh-water period of life. Nippon Suisan Gakkaishi 40: 669–706. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3371, 1975)

OTA, T., AND M. YAMADA. 1974. Lipids of Masu Salmon. III. Differences in the lipids of residual type and seaward migration type of Masu salmon parr during the period of seaward migration. Nippon Suisan Gakkaishi 40: 707–713. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3372, 1975)

CUMONT, G., G. VIALLEX, H. LELIÈVRE, AND P. BOBENRIETH. 1972. Mercury contamination in sea fish. Rev. Int. Oceanogr. Med. 28: 95–127. (Transl. from French by Fish. Mar. Serv. Transl. Ser. No. 3373, 1975)

KAMIYAMA, S., AND M. SAKURAI. 1974. The chemistry of chlorostyrene and its applications. Kagaku Kogyo 25: 38–43. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3374, 1975)

HIRAYAMA, K. 1966. Studies on water control by filtration through sand bed in a marine aquarium with closed circulating system. IV. Rate of pollution of water by fish, and the possible number and weight of fish kept in an aquarium. Nippon Suisan Gakkaishi 32: 20–27. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3375, 1975)

CHARNIAUX-COTTON, H. 1974. Physiology of invertebrates. New data on the vitellogenesis of malacostracan crustaceans based on the amphipod *Orchestia gammarellus* (Pallas): follicle formation from permanent tissue; busulfan's action; the inhibiting action of the juvenile hormone. C. R. Acad. Sci., Ser. D. 279: 563–566. (Transl. from French by Fish. Mar. Serv. Transl. Ser. No. 3376, 1975)

RZHAVSKAYA, F. M., AND T. A. DUBROVSKAYA. 1972. Separation of fat from sterilized liver of codfish for determining the fatty acid composition. Tr. Vses. Nauchno-Issled. Inst. Morsk. Rybn. Khoz. Okeanogr. 88: 112–124. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3377, 1975)

Prabucki, A. L. 1973. Technological significance of invisible fats and lipids in food of animal origin. Wiss. Veroeff. Dtsch. Ges. Ernaehr. 24: 100–103. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3378, 1975)

Erokhin, V. E. 1974. The role of external organic metabolites of algae in the energy budget of certain marine invertebrates. Biologicheskaya produktivnost' yuzhnykh morei 1974: 111–120. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3379, 1975)

Klokov, V. K. 1973. The dynamics of chum salmon abundance in various northern coastal areas of the Okhotsk Sea. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 86: 66–80. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3380, 1975)

Ziemlanski, S., D. Cieslakowa, G. Okolska, and B. Kucharczyk. 1974. Absorption from the alimentary tract of selected fatty acids of rapeseed oil. Przegl. Lek. 31: 322–327. (Transl. from Polish by Fish. Mar. Serv. Transl. Ser. No. 3381, 1975)

Petipa, T. S., A. V. Monakov, A. P. Pavlyutin, and Yu. I. Sorokin. 1974. Nutrition and energy balance of tropical copepods. Biologicheskaya produktivnost' yuzhnykh morei 1974: 136–152. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3382, 1975)

Zaika, V. E. 1974. The relationship between the production and metabolism of a population. Biologicheskaya produktivnost' yuzhnykh morei 1974: 100–111. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3383, 1975)

Lopez-Benito, M. 1972. Use of sodium hydroxide in canning mackerel, horse mackerel and sardines. Inf. Tec. Inst. Invest. Pesque. 1: 3–19. (Transl. from Spanish by Fish. Mar. Serv. Transl. Ser. No. 3384, 1975)

Ovsyannikov, I. I. 1974. The sonar method used by TINRO in estimating the density of commercial fish concentrations. Document submitted by USSR to the Canada–USSR Meetings on Fisheries in Moscow-Batumi, USSR, November 1974. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3385, 1975)

Efimov, Y. N. 1974. Size of Pacific hake stocks and the state of their fishery. Document submitted to the Canada–USSR Meetings on Fisheries in Moscow-Batumi, USSR, November 1974. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3386, 1975)

Pekkala, S., B. Holmbom, and E. Avela. 1974. Aspects on the preparation and application of capillary gas chromatography columns. Kem.-Kemi 1: 25–29. (Transl. from Swedish by Fish. Mar. Serv. Transl. Ser. No. 3387, 1975)

Lisovskaya, V. I. 1973. The composition of lipids in the red and white muscles of mackerel (*Trachurus mediterraneus ponticus*) and anchovy (*Engraulis encrasicholus ponticus*) in the northwestern part of the Black Sea. Mater. Vses. Simp. Izuch. Chern. Sredizemogo Morei 2: 142–145. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3388, 1975)

Marumo, R., and K. Kamada. 1973. Oil globules and their attached organisms in the east China Sea and the Korushio area. Nippon Kaiyo Gakkai-Shi 29: 155–158. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3389, 1975)

Kanekatsu, R. 1972. Amylase in the digestive juice of silkworm, *Bombyx* mori. Nippon Sanshigaku Zasshi 41: 445–451. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3390, 1975)

Blanchet, M.-F. 1974. Experimental biology. C.R. Acad. Sci., Ser. D, 278: 509–512. (Transl. from French by Fish. Mar. Serv. Transl. Ser. No. 3391, 1975)

Nagasawa, S., and R. Marumo. 1967. Taxonomy and distribution of *Trichodesmium* (Cyanophyceae) in the Kuroshio water. Nihon Purankuto Kenkyu Renrakukai Ho 1967 139–144. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3392, 1975)

Shul'man, G. Ye. 1969. Relationship between size and fat accumulation in certain fish of the southern seas. Biol. Nauki 12: 5–8. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3393, 1975)

Afzalpurkar, A. B., and H. K. Mangold. 1971. Rapeseed as fish food. Annu. Rep. Fed. Centre Lipid Res: 22 p. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3394, 1975)

Afanasyev, V. I., and L. N. Kharchenko. 1974. Change in the composition of fatty acids during red spot disease of carp. Veterinariya (Moscow) 7: 62–64. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3395, 1975)

Lankin, V. Z., S. P. Anikeyeva, A. A. Ananenko, and Yu. Ye. Vel'tishchev. 1974. Quantitative determination of unesterified fatty acids in blood serum using the method of gas-liquid chromatography. Vopr. Med. Khim. 20: 435–439. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3396, 1975)

Grybauskiene, V., M. Jamontiene, and K. Jankevicius. 1973. Activity of hydrolytic enzymes in the water and plankton biomass of a eutrophic body of water, the Courland Lagoon. Liet. TSR Mokslu Akad. Darb., Ser. C, 2: 3–7. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3397, 1975)

Koganezawa, A., N. Ishida, K. Suzuki, K. Goto, and H. Abe. 1968. Studies on the growth of fingerling dog salmon (*Oncorhynchus keta*) in relation to salinity. Miyagi-ken suisanshikenjo kenkyu hokoku dai yon go betsuzuri 4: 1–6. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3398, 1975)

Yamauchi, Y., and Y. Shimizu. 1973. Recently discussed problems on the safety of fluorescent dyestuff with regard to the human body. Senryo To Yakuhin 18: 279–287. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3399, 1975)

Dimitrov, G. 1974. Determination of volatile fatty acids in rumen by gas chromatography. Zhivotnovud. Nauki 11: 131–136. (Transl. from Bulgarian by Fish. Mar. Serv. Transl. Ser. No. 3400, 1975)

Anon. 1974. Results of Japanese squid fishery experiments in the Northwest Atlantic, 1973. Kaiyo Suisan Shigen Kaihatsu Senta 48: 1–131. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3401, 1975)

Chernyavskii, V. I. 1973. Some problems in predicting the type of thermal conditions in the Sea of Okhotsk. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 86: 49–55. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3402, 1975)

Kobayashi, M., S. Okauchi, F. Nakazawa, and S. Noguchi. 1974. Fatty acid composition of 14 kinds of deep-sea fish oils. Kaseigaku Zasshi 25: 580–583. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3403, 1975)

Tosev, A. 1974. Investigation of volatile fatty acids in the blood of sheep. Zhivotnovud. Nauki 11: 125–130. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3404, 1975)

Bregman, Yu. E. 1971. Relationship between the metabolic rate and the growth rate in the sea urchin *Strongylocentrotus intermedius* (Echinodermata, Strongylocentrotodae). Zool. Zh. 50: 1530–1538. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3405, 1975)

Noguchi, S., F. Nakazawa, J. Fukushima, and M. Kobayashi. 1974. A new method of gas chromatographic analysis of fatty acid and its application to oils of shell fish. Kaseigaku Zasshi 24: 699–703. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3406, 1975)

Verbruggen, M. 1970. A process for imparting or conserving a natural coloration in foods. Deutsches Patentamt, Offenlegunsschrift: 1–6. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3407, 1975)

Pastukhov, V. D. 1965. A contribution to the methodology of counting Baikal seal. Morskie mlekopitayushchie 100: 100–104. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3408, 1975)

Tomioka, K., J. Ogushi, and K. Endo. 1974. Studies on dimethylamine in food. II. Concerning the enzymic formation of dimethylamine. Nippon Suisan Gakkaishi 40: 1021–1026. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3409, 1975)

Takahashi, Y. 1974. Yearly variations in the relative catchability of the fishing vessels operations with the mothership pollock fishery in the eastern Bering Sea. Bull. Far Seas Fish. Res. Lab. 10: 1–25. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3410, 1975)

Bhaud, M. 1974. Estimating net level when sampling plankton in coastal waters. Vie Milieu 24: 93–108. (Transl. from French by Fish. Mar. Serv. Transl. Ser. No. 3411, 1975)

Ringen, J. 1939. The feed value of seaweed meal. Inst. Husdyrernaering Foringslaere Nor. Landbrukshogsk. 3: 1–8. (Transl. from Norwegian by Fish. Mar. Serv. Transl. Ser. No. 3412, 1975)

Kruger, F. 1973. The mathematics of animal growth. Helgol. Wiss. Meeresunters. 25: 509–550. (Transl. from German by Fish. Mar. Serv. Transl. Ser. No. 3413, 1975)

Okanazawa, A. 1970. Sea surface of salmon and trout and related problems. Suisan Kaigyo Kenkyu Kaiho 17: 95–101. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3414, 1975)

Koganezawa, A., F. Yoshida, N. Ishida, K. Goto, and A. Ito. 1971. Studies on the culture of salmonoid fishes in sea water. I. Acclimatization of salmonoid fishes to sea water. Miyagi-Ken Suidan Shikenjo Kenkyu Hokoku 5: 10 p. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3415, 1975)

Brinchmann, H. J. 1967. Pigmentation of pond-reared fish. Nor. Tek. Høgskole: 1–32. (Transl. from Norwegian by Fish. Mar. Serv. Transl. Ser. No. 3416, 1975)

Hikita, H., M. Miyata, and S. Ishikawa. [Undated]. Experimental study of chronic organophosphate (OP) intoxications in beagle dogs. Activities of cholinesterase and residue of OP. Nippon Ganka Gakkai Zasshi 77: 1254–1265. (Transl. from Japanese by Fish. Mar. Serv. Transl. Ser. No. 3417, 1975)

Jankovsky, M., P. Bobak, and J. Hubacek. 1974. Evaluation of the methods of preparation of fatty acid esters for their determination by gas chromatography. Chem. Listy 68: 858–866. (Transl. from Czechoslovakian by Fish. Mar. Serv. Transl. Ser. No. 3418, 1975)

Nesterov, G. A. 1973. Experiments in the use of sleep-inducing agents and ditiiline in the harvesting of harp seals. Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 87: 219–225. (Transl. from Russian by Fish. Mar. Serv. Transl. Ser. No. 3419, 1975)

List of Establishments

(1) Department of the Environment
Fisheries and Marine Service
Pacific Biological Station
P.O. Drawer 100
Nanaimo, British Columbia V9R 5K6
(2) Department of the Environment
Fisheries and Marine Service
Vancouver Laboratory
6640 N.W. Marine Drive
Vancouver, British Columbia V6T 1X2
(3) Department of the Environment
Fisheries and Marine Service
Pacific Environment Institute
4160 Marine Drive
West Vancouver, British Columbia V7V 1N6
(4) Department of the Environment
Fisheries and Marine Service
Freshwater Institute
501 University Crescent
Winnipeg, Manitoba R3T 2N6
(5) Department of the Environment
Fisheries and Marine Service
Arctic Biological Station
P.O. Box 400
Ste. Anne de Bellevue, Quebec H9X 3L6
(6) Department of the Environment
Fisheries and Marine Service
Biological Station
St. Andrews, New Brunswick E0G 2X0
(7) Department of the Environment
Fisheries and Marine Service
Marine Ecology Laboratory
Bedford Institute
P.O. Box 1006
Dartmouth, Nova Scotia B2Y 4A2
(8) Department of the Environment
Fisheries and Marine Service
Halifax Laboratory
P.O. Box 429
Halifax, Nova Scotia B3J 2R3
(9) Department of the Environment
Fisheries and Marine Service
Biological Station
St. John's, Newfoundland A1C 5X1
(10) Department of the Environment
Fisheries and Marine Service
Office of the Editor
116 Lisgar Street
Ottawa, Ontario K1A 0H3
(11) Department of the Environment
Fisheries and Marine Service
Canada Centre for Inland Waters
Great Lakes Biolimnology Laboratory
P.O. Box 5050
867 Lakeshore Rd.
Burlington, Ontario L7R 4A6
(12) Department of the Environment
Fisheries and Marine Service
Atlantic Regional Office,
Director's Committee
1 Sackville Place P.O. Box 159
Halifax, Nova Scotia B3J 2M4

Liste d'établissements

(1) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Station biologique du Pacifique
C.P. 100
Nanaïmo (Colombie-Britannique) V9R 5K6
(2) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Laboratoire de Vancouver
6640 nord-ouest, prom. Marine
Vancouver (Colombie-Britannique) V6T 1X2
(3) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Institut de l'environnement du Pacifique
4160, prom. Marine
Vancouver-Ouest (Colombie-Britannique)
V7V 1N6
(4) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Institut des eaux douces
501. University Crescent
Winnipeg (Manitoba) R3T 2N6
(5) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Station biologique de l'Arctique
C.P. 400
Sainte-Anne-de-Bellevue (Québec) H9X 3L6
(6) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Station biologique
St. Andrews (Nouveau-Brunswick) E0G 2X0
(7) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Laboratoire d'écologie marine
Institut de Bedford C.P. 1006
Dartmouth (Nouvelle-Ecosse) B2Y 4A2
(8) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Laboratoire d'Halifax
C.P. 429
Halifax (Nouvelle-Ecosse) B3J 2R3
(9) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Station biologique
Saint-Jean (Terre-Neuve) A1C 5X1
(10) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Bureau du rédacteur
116, rue Lisgar
Ottawa (Ontario) K1A 0H3
(11) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Centre canadien des eaux intérieures
Laboratoire de biolimnologie des Grands Lacs
C.P. 5050
867, ch. Lakeshore
Burlington (Ontario) L7R 4A6
(12) Ministère de l'Environnement
Service des pêches et des sciences de la mer
Bureau régional de l'Atlantique,
Comité du directeur
1 Place Sackville C.P. 159
Halifax (Nouvelle-Ecosse) B3J 2M4

ADDITIONAL PUBLICATIONS / PUBLICATIONS ADDITIONNELLES

The Service also publishes a series of *Bulletins*, each on a specific topic. These are for sale by Information Canada, Ottawa, and remittances must be in advance, payable in Canadian funds to the order of the Receiver General of Canada. *Bulletins* are also available from local booksellers and Information Canada bookshops throughout Canada.

The *Annual Report* of the Board and the biennial *Review* of investigations are available free, on request. All publications may be referred to at establishments located at: Ottawa, Ont.; Nanaimo, Vancouver, and West Vancouver, B.C.; Winnipeg, Man.; Ste. Anne de Bellevue, Que.; St. Andrews, N.B.; Halifax and Dartmouth, N.S.; and St. John's, Nfld.

Le Service publie également une série de *Bulletins*, chacun traitant sur un sujet spécifique. Les publications de l'ORP sont vendues par Information Canada à Ottawa. Les remises, payables d'avance en monnaie canadienne, doivent être établies à l'ordre du Receveur général du Canada. Les *Bulletins* sont aussi en vente chez votre libraire et dans les librairies d'Information Canada.

Vous pouvez obtenir le Rapport Annuel et la Revue biennale gratuitement. On peut consulter ces ouvrages aux établissements situés à Ottawa (Ont.), à Nanaïmo, à Vancouver, et à Vancouver Ouest (C.-B.), à Winnipeg (Man.), à Ste-Anne-de-Bellevue (P.Q.), à St-Andrews (N.-B.), à Halifax et à Dartmouth (N.-E.), et à St-Jean (T.-N.).

Journal
of the Fisheries
Research
Board
of Canada

Guide for Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

CONTENT

We invite submission of manuscripts in the broad field of fisheries management, ocean science, and aquatic environments relevant to Canada.

Articles: Reports of research studies of broad scope that are original contributions to science.

Notes: Differ from papers on the basis of scope or completeness, rather than quality of research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on methodology or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as articles except that they have no centered headings and should occupy no more than four printed pages.

Reviews: Detailed articles that are critical appraisals of broad areas of investigation, particularly in fields that have shown rapid development in recent years.

Perspectives: Essays of opinion or hypothesis on fisheries, ocean science, aquatic environments, or related topics that are of concern to the professional and layman. References are desirable; informal style is welcomed.

Letters: Opinion on topics recently under discussion in the *Journal*; preferred maximum length, 500 words. The Editor reserves the right to shorten letters and to make other changes to accord with the style of the *Journal*.

EDITORIAL PRACTICES

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW., Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (Third Edition, 1970) Special Publication No. 6 of the American Fisheries Society.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, the essentials of the new knowledge, and the main conclusions. Abstracts are published in English and French; those submitted in one language only are translated by the *Journal*.

The Editor normally submits each manuscript to at least two *referees*. Contributors are encouraged to suggest at least four names to be added to the list from which referees may be selected.

Illustrations should be submitted in triplicate as photographs (*glossy prints*) no larger than a standard page and must accompany the manuscript. Prints should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to the appropriate size. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting only errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent out with the galley proof). All orders should be sent to the Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8. Invoices relating to the reprints will be sent out by the Printer. A charge of $30.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

CHECKLIST ON MANUSCRIPTS

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

Journal
de l'office
des recherches
sur les pêcheries
du Canada

Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

SUJETS

Nous désirons reçevoir des manuscrits s'insérant dans le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada.

Articles: Comptes rendus d'études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent traiter de problèmes particuliers et bien définis; de travaux qui sont en grande partie confirmatoires; de méthodologie ou de techniques de recherche; de progrès de la connaissance découlant d'études plus vastes; de développements dans des projets abandonnés; ou de découvertes préliminaires qui méritent d'être publiées avant la solution de problèmes à l'étude. Les notes peuvent être présentées d'une façon aussi souple que les articles, mais elles ne doivent pas porter d'en-têtes centrés ni occuper plus de quatre pages.

Critiques: Articles détailés constituant une appréciation critique de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais de l'opinion ou de l'hypothèse sur les pêches, les sciences de la mer, les milieux aquatiques, ou sur des sujets connexes qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres: Opinions sur des sujets exposés dans le *Journal*. Longueur maximale préférable: 500 mots. Le directeur se réserve le droit de raccourcir les lettres et de faire d'autres modifications dans le style du *Journal*.

DISPOSITIONS GÉNÉRALES

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de photos (*sur papier glacé*), ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauter lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de la facturer. Les frais sont de $30.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

LISTES DE CONTRÔLES POUR MANUSCRITS

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal
of the Fisheries
Research
Board
of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize only the first word and proper names and adjectives. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send at least 3 *glossy prints* (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal
de l'office
des recherches
sur les pêcheries
du Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, ne nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, et y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie et ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés.*

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit trois photos *sur papier glacé* (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

Canadian Conference For Fisheries Research

The twenty-ninth Annual Meeting of the CCFFR will be held at the Holiday Inn, Ottawa, January 5 and 6, 1976. The Fisheries Research Board of Canada and the Fisheries and Marine Service, Department of the Environment, will again sponsor this meeting. The President is H. H. Harvey, University of Toronto, Toronto, the Secretary is J. C. Stevenson, and the Treasurer is J. Camp, both of the Fisheries and Marine Service, Department of the Environment, Ottawa. Program Chairman is W. C. Leggett, McGill University, Montreal.

The Canadian Society of Environmental Biologists will also meet at Ottawa, January 7, 1976.

CCFFR Program

Monday January 5

Morning Session — The optimum sustained yield concept and its application to Canadian fisheries

Convener:
W. E. Ricker
Department of the Environment
Fisheries and Marine Service
Pacific Biological Station
P.O. Drawer 100
Nanaimo, B.C.

Afternoon Session — The physiological basis of fish migration

Conveners:
F. W. Beamish
Department of Zoology
University of Guelph
Guelph, Ontario
and
W. C. Leggett
Department of Biology
McGill University
Montreal, Quebec

Evening — Smoker sponsored by the National Museum of Natural Sciences, National Museums of Canada, Victoria Memorial Museum Building, 3rd Floor Lounge, 8:30 pm.

Tuesday, January 6

Morning Session — Educational requirements for biologists in Canada

Convener:
J. R. Vallentyne
Department of the Environment
Fisheries and Marine Service
Freshwater Institute
501 University Crescent
Winnipeg, Manitoba

Afternoon Session — Contributed papers

Convener:
D. B. Lister
Department of the Environment
Resource Development Branch
Maritimes Region
P.O. Box 550
Halifax, Nova Scotia

Conférence canadienne pour la recherche sur le pêches

La vingt-neuvième réunion annuelle aura lieu, les 5 et 6 janvier 1976 au Holiday Inn, à Ottawa. Elle sera à nouveau parrainée par l'Office des recherches sur les pêcheries du Canada et le Service des pêches et des sciences de la mer du ministère de l'Environnement. Le président en est M. H. H. Harvey, de l'Université de Toronto, Toronto, le secrétaire, M. J. C. Stevenson et le trésoirier, M. J. Camp, tous deux du Service des pêches et des sciences de la mer du Ministère, le président du programme, M. W. C. Leggett de l'université McGill, Montréal.

La "Canadian Society of Environmental Biologists" se réunira aussi à Ottawa, le 7 janvier 1976.

Programme de la conférence

Lundi 5 janvier

Séance du matin — La notion de rendement soutenu optimal et son application aux pêches canadiennes

Convocateur:
W. E. Ricker
Ministère de l'Environnement
Service des pêches et des sciences de la mer
Station de Biologie du Pacifique
C. P. 100
Nanaimo (C.-B.)

Séance de l'apres midi — Les bases physiologiques de la migration des poissons

Convocateurs:
F. W. Beamish
Department de Zoologie
Université de Guelph
Guelph (Ontario)
et
W. C. Leggett
Department de Biologie
Université McGill
Montréal (Québec)

Soirée — Réunion amicale parrainée par le Musée national des sciences naturelles, Musées nationaux du Canada, Edifice du Victoria Memorial Museum, salle de réception du 3ième étage, 8:30

Mardi 6 janvier

Séance du matin — Connaissances nécessaires aux biologistes du Canada

Convocateur:
J. R. Vallentyne
Ministère de l'Environnement
Institut des eaux douces
501, University Crescent
Winnipeg (Manitoba)

Séance de l'après-midi — Communications à la Conférence

Convocateur:
D. B. Lister
Ministère de l'Environnement
Direction du développement des ressources
Région des Maritimes
C. P. 550
Halifax (Nouvelle-Ecosse)

Invitation for the Submission of Papers
8th International Conference on Water Pollution Research

Sydney, Australia
October 17–22, 1976

Technical sessions will provide for the presentation and discussion of selected papers on original research and development on a wide variety of topics related to marine and freshwater pollution and wastewater treatment. Instantaneous translation services — English, French and German — will be available.

Workshop sessions will review progress and discuss current problems on the following subjects:
- Water resource quality management
- Marine and estuarine waste disposal
- Ultimate disposal of solid and liquid wastes
- Land surface and subsurface disposal of wastewater

Technical visits will be conducted on an afternoon free of sessions, to wastewater treatment plants and other places of technical interest.

RANGE OF TOPICS
GROUP
NUMBER

1. Chemical quality standards and their determination.
2. Biological monitoring parameters and their characterization.
3. Public health aspects, virology, disinfection.
4. Biocides, pollutant accumulation in macro-organisms.
5. Fish studies.
6. Stream analysis — modelling — river management.
7. Eutrophication — chemical and biological aspects.
8. Marine ecology.
9. Estuarine pollution — surveys.
10. Pipeline disposal to sea.
11. Pollution from oil and offshore materials resources development.
12. Groundwater quality studies.
13. Sewerage overflows, storm water storage and treatment.
14. Sedimentation, sludge characteristics and thickening.
15. Sludge: dewatering, incineration, land disposal.
16. Anaerobic processes, digestion, septic tanks.
17. Practical aspects of activated sludge process, nitrification, denitrification, simultaneous phosphorus removal.
18. Aeration systems, oxygen plants.
19. Trickling filter, high rate plastic media, rotary discs.
20. Advanced wastewater treatment, physicochemical processes, case studies of operation.
21. Large treatment plants.
22. Small treatment plants, rural problems, land treatment, lagoons, transient population communities.
23. Industrial wastes — farm, agricultural, food process.
24. Industrial wastes — petrochemical, synthetic organics, paper pulp.
25. Industrial wastes — inorganic — toxicants — non biodegradable.
26. Water quality network control.
27. Miscellaneous — papers of wide general interest not covered within above specific categories.

For further information contact:
Conference Secretariat
G.P.O. Box 2609
Sydney 2001, N.S.W.
Australia

Appel aux spécialistes
la 8^{e} Conférence internationale sur la recherche en pollution des eaux

Sydney, Australie
du 17 au 22 octobre 1976

Les séances d'information donneront lieu à la présentation de documents choisis faisant état de travaux de recherche et de développement en matière de pollution des eaux douces et salées et de traitement des eaux usées, ainsi qu'à des discussions. Des interprètes vers l'anglais, le français et l'allemand seront sur les lieux.

Il y aura des ateliers sur les progrès accomplis et sur les problèmes actuels concernant:
- la gestion des ressources en eau, du point de vue de leur qualité;
- les divers aspects de l'évacuation des déchets dans la mer et les estuaires;
- la destination finale des déchets solides et liquides; et
- l'évacuation sur le sol ou dans le sol des eaux usées

Il y aura visite organisée d'installations de traitment des eaux usées et d'autres endroits intéressants du point de vue technique, au cours d'une après-midi ilbre.

LISTE DES SUJETS PAR CATÉGORIES
CLASSIFICATION

1. Normes de qualité chimique et leur détermination.
2. Paramètres de contrôle biologiques et leur caractérisation.
3. Aspects d'hygiène publique, virologie, désinfection.
4. Biocides, accumulation de polluants dans les macro-organismes.
5. Études ichtyologiques.
6. Analyse des cours d'eau, établissement de modèles, gestion.
7. Aspects chimiques et biologiques de l'eutrophisation.
8. Écologie marine.
9. Pollution des estuaires et son étude.
10. Evacuation des déchets en mer par pipeline.
11. Pollution par les hydrocarbures et pollution liée à l'exploitation "offshore" des ressources naturelles.
12. Études de la qualité des eaux souterraines.
13. Débordements d'eaux d'égout, entreposage et traitement des eaux pluviales.
14. Décantation, caractéristiques et épaississement des boues.
15. Déshydratation, incinération et épandage des boues.
16. Procédés anaérobies, digestion et fosses septiques.
17. Côtés pratiques des procédés d'épuration par boues activées, nitrification, dénitrification, élimination simultanée du phosphore.
18. Dispositifs d'aération, installations d'oxygénation.
19. Lits bactériens, résines à grand rendement, disques biologiques.
20. Traitements nouveaux des eaux usées, procédés physicochimiques, étude de cas-types.
21. Grosses installations de traitement.
22. Petites installations de traitement, problèmes ruraux, épandage des eaux usées, lagunes, populations mobiles.
23. Déchets industriels, produits par l'élevage, l'agriculture, l'industrie alimentaire.
24. Déchets produits par les industries pétroléochimiques, des substances organiques de synthèse et des pâtes à papier.
25. Déchets produits par l'industrie chimique minérale, des produits toxiques et non biodégradables.
26. Réseaux de surveillance de la qualité de l'eau.
27. Divers — Communications d'intérêt général qui n'entrent pas dans les catégories mentionnées plus haut.

Pour plus de renseignements, écrire au:
Secrétariat de la Conférence
B.P. 2609
Sydney 2001 (N.S.W.)
Australie

Perspectives

The Fisheries Research Board of Canada — seventy-five years of achievements **W. E. Ricker** 1465–1490

Letters/Lettres

Linear regressions in fishery research: some comments **P. Jolicoeur** 1491–1494

A note concerning Professor Jolicoeur's comments **W. E. Ricker** 1494–1498

Book Reviews/Comptes rendus

Color atlas of the diseases of fishes, amphibians and reptiles (E. Elkan and H. Reichenback-Klinke) **G. R. Bell** 1499

Review of fisheries of the North Pacific (R. J. Browning) **W. F. Royce** 1500

Algal physiology and biochemistry (W. D. P. Stewart) **N. J. Antia** 1500–1501

Pollution ecology of freshwater invertebrates (C. W. Hart Jr. and S. L. H. Fuller) **H. B. N. Hynes** 1501–1502

Obituary — Albert Lewis Tester 1908–1974 **J. C. Stevenson and W. A. Gosline** 1503–1504

Coming next month/À paraître le mois prochain 1507

Recent publications/Récentes publications 1508–1516

Additional publications/Publications additionnelles 1517

Guide for authors and typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–v*

© Information Canada, Ottawa, 1975

Journal
of the Fisheries
Research
Board
of Canada

Journal
de l'office
des recherches
sur les pêcheries
du Canada

JFRBAK32(8)1243–1517(1975)

Volume 32, No. 8, August 1975

Volume 32, n° 8, août 1975

Bacterial diseases of fishes: diagnostic procedures for gram-negative pathogens **E. B. Shotts Jr. and G. L. Bullock** 1243–1247
Isolation and identification of constituents toxic to juvenile rainbow trout (*Salmo gairdneri*) in caustic extraction effluents from kraft pulpmill bleach plants **J. M. Leach and A. N. Thakore** 1249–1257
Passage of fish eggs through a pumped storage generating station **D. E. Snyder** 1259–1266
Fish viruses — survival and inactivation of infectious pancreatic necrosis virus **R. M. MacKelvie and D. Desautels** 1267–1273
Limited arsenic dispersion in sea water, sediments, and biota near a continuous source **W. R. Penrose, R. Black, and M. J. Hayward** 1275–1281
Summerkill risk in prairie ponds and possibilities of its prediction **J. Barica** 1283–1288
Characterization and subcellular localization of leucine aminonaphthylamidase (LAN) in rainbow trout (*Salmo gairdneri*) **G. R. Bouck, P. W. Schneider Jr., J. Jacobson, and R. C. Ball** 1289–1295
Uptake of mercury by freshwater clams (family Unionidae) **A. L. Smith, R. H. Green, and A. Lutz** 1297–1303
Spatial model for an exploited shellfish population, and its application to the Georges Bank scallop fishery **J. F. Caddy** 1305–1328
Metabolism of pyruvate in postmortem adductor muscle of the sea scallop (*Placopecten magellanicus*) during iced storage **M. Sakaguchi, D. F. Hiltz, and W. J. Dyer** 1329–1337
Relative importance of food and water in long-term zinc^{-65} accumulation by marine biota **W. C. Renfro, S. W. Fowler, M. Heyraud, and J. La Rosa** 1339–1345
Migrations and biological characteristics of Atlantic mackerel (*Scomber scombrus*) occurring in Newfoundland waters **J. A. Moores, G. H. Winters, and L. S. Parsons** 1347–1357
Movement, growth, and survival in a stream population of wild brook trout (*Salvelinus fontinalis*) during a period of removal of non-trout species **W. A. Flick and D. A. Webster** 1359–1367
A revised interpretation of the Skeena River sockeye salmon (*Oncorhynchus nerka*) **W. E. Ricker and H. D. Smith** 1369–1381
Changes in abundance and certain biological characteristics of Grand Bank American plaice (*Hippoglossoides platessoides*) **T. K. Pitt** 1383–1398
Sedimentation of organic matter in St. Margaret's Bay, Nova Scotia **T. J. M. Webster, M. A. Paranjape, and K. H. Mann** 1399–1407
Summer distribution of the nearshore fish community near a thermal generating station as determined by acoustic census **J. R. M. Kelso and C. K. Minns** 1409–1418
Size selective predation by juvenile chum salmon (*Oncorhynchus keta*) on epibenthic prey in Puget Sound **R. J. Feller and V. W. Kaczynski** 1419–1429
Cholesterol requirements of juvenile American lobster (*Homarus americanus*) **J. D. Castell, E. G. Mason, J. F. Covey** 1431–1435

Notes

Possible interference in the isolation of IPN virus from carrier fish **B. L. Nicholson and R. Dexter** 1437–1439
Life history observations on the Puget Sound rockfish, *Sebastes emphaeus* (Starks, 1911) **L. L. Moulton** 1439–1442
Distribution of hyperiid amphipods off the Oregon coast **H. V. Lorz and W. G. Pearcy** 1442–1447
Young witch flounder, *Glyptocephalus cynoglossus*, on the slope off Virginia **D. Markle** 1447–1450
Preheat treatment for improvement of frozen storage stability at −10 C in fillets and minced flesh of silver hake (*Merluccius bilinearis*) **B. S. Lall, A. R. Manzer, and D. F. Hiltz** 1450–1454
Comparative toxicity of larval lampricide (TFM: 3-trifluoromethyl-4-nitrophenol) to selected benthic macroinvertebrates **A. W. Maki, L. Geissel, and H. E. Johnson** 1455–1459
Hepatic morphology and acid phosphatase localization in the channel catfish (*Ictalurus punctatus*) **M. W. Kendall and W. E. Hawkins** 1459–1464

(Continued inside back)